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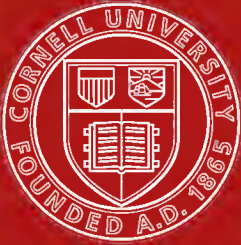
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AN OUTLINE OF PSYCHOBIOLOGY

BY

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1914

L.V.

TO
GEORGE M. STRATTON

PREFACE.

THIS outline is intended to aid those students of psychology who have had no courses in biology covering the morphological and physiological data which are directly contributory to psychology. It is designed to convey the elementary information which is absolutely necessary, and to stimulate the student to further reading. Since the time which a psychologist can give to the study of biology is narrowly limited, it is essential that strong emphasis should be placed on such details as are of the greatest psychological significance, although this results in a treatment which, from the physiological point of view, is extremely unbalanced.

Heretofore, psychologists who have recognized the value of physiology have confined their attention almost exclusively to neurology. This neurology has been of little use to the psychologist, except as a terminological scheme in which he could restate his psychological facts and speculations. Of late it has been becoming clear that the pressing need in psycho-physiology is for the study of muscle and gland, and that only through the study of these tissues in their structural and functional relation to nervous tissue can neurology be made psychologically valuable. It is this point of view which has dominated the preparation of this outline.

I hope that this book, which was prepared primarily for the use of my own classes, may be of service to other psychologists, at least until a more systematic and comprehensive text becomes available. Since it is, at the time of writing, the first book of its kind, it is entitled to the credit, and also to the leniency usually extended to pioneers.

The cuts which accompany the text are from various sources. Some are familiar from having appeared in many places. I am much indebted to those who have kindly given me permission to use or reproduce their illustrations, especially to Dr. Ramon y Cajal, and to the authors, editors, and publishers of Bailey's *Histology* and Cunningham's *Anatomy* (William Wood and Co., New York); Lewis and Stöhr's *Histology* (P. Blakiston's Son & Co., Philadelphia); Quain's *Anatomy* (Eleventh Edition, Longmans, Green and Co., New York); Barker's *The Nervous System* (D. Appleton & Co., New York); and Toldt's *Atlas of Human Anatomy* (Rebman and Co., New York).

The lists of references appended to each chapter is merely typical.

There are many books in which the student may find helpful material by consulting the indices. The books mentioned above are especially good. The histologies by Lewis and Stöhr and by Bailey are well suited to beginners. Schäfer's *Microscopic Anatomy* (Vol. II, Part I, of Quain's *Anatomy*), Cunningham's *Anatomy*, Howell's *Physiology*, Starling's *Physiology*, and Barker's *The Nervous System* should be in the reference library available to the student. The Yearly *Psychological Index* and the monthly topical reviews in the *Psychological Bulletin* are the most efficient guides to recent psychological and psycho-physiological literature.

For the benefit of those students to whom the technical terms in the text will be new, the proper stress in pronunciation of some of these terms is indicated in the index.

I am under obligations to a number of persons who have given me assistance in the preparation of this book, especially to Dr. Herbert M. Evans, Dr. Caswell Grave, and Dr. S. O. Mast of the Johns Hopkins University and Dr. Percy W. Cobb of Nela Research Laboratory, who have helped me with suggestions and criticisms, and to Dr. Warner Brown of the University of California, Dr. H. M. Johnson of Nela Research Laboratory, and Dr. George R. Wells of Oberlin College, who have done the unpleasant work of reading the proof.

K. D.

THE JOHNS HOPKINS UNIVERSITY, OCTOBER 15, 1914.

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AN OUTLINE OF PSYCHOBIOLOGY

CHAPTER I.

THE CELL.

THE smallest unit of living tissue, both plant and animal, is the *cell*. Every organism is a cell, a group of cells, or an aggregate of cells with certain other structures produced directly by the activity of cells. Some plants, and some animals, consist permanently of a single cell each. Every plant and every animal commences its individual life as a single cell. These unicellular organisms possess, in a limited way, the functioning capacities of more complex organisms. The study of any form or function of living tissue may therefore advantageously begin in a study of the cell. [Fig. 1.]

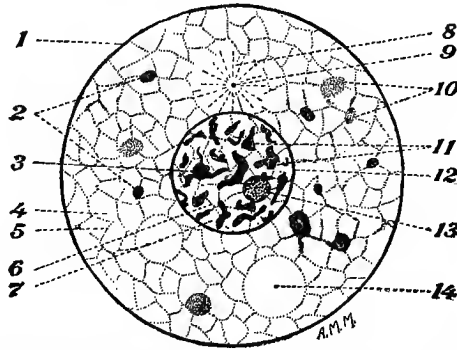


FIG. 1. Diagram of typical cell. (Bailey, *Histology*.) 1. Cell membrane. 2. Granules of metaplast. 3. Net-knob, or karyosome. 4. Hyaloplasm. 5. Spongio-plasm. 6. Linin net-work. 7. Nucleoplasm. 8. Attraction-sphere. 9. Centrosome. 10. Plastids. 11. Chromatin net-work. 12. Nuclear membrane. 13. Nucleolus. 14. Vacuole.

The cell has been defined as “a mass of protoplasm containing a nucleus.”¹ It is true, we find certain cells, the red blood corpuscles of mammals [Fig. 3] which, during the period of their special functional activity, have no nucleus. These cells, however, have finished their growth, and die without issue; during their period of growth they are nucleated.

¹ Leydig, *Lehrbuch der Histologie*, 1857, S. 9.

The typical life-history of a cell has been epitomized in the statement that "both nucleus and cytoplasm arise through the division of the corresponding elements of a preëxisting cell",² or, more succinctly, "*Omnis cellula e cellula*".³

Protoplasm is not a single definite substance, but varies greatly from cell to cell. The protoplasm of a nerve cell, for example, is different from that of a liver cell. The **nucleus** of any cell, moreover, differs physically and chemically from the remaining protoplasm of the cell. The chemical structure of protoplasm is in any case exceedingly complex, the chief constituents in point of quantity being carbon, oxygen, nitrogen, hydrogen, sulfur, fosphorus, chlorin, sodium, potassium, calcium, magnesium, and iron. Certain organisms include still other elements in their protoplasm.

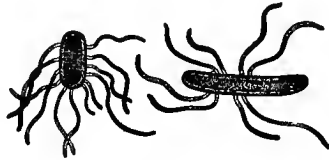


FIG. 2. Ciliated cells; bacilli of typhoid fever. (Sedgwick and Wilson, *General Biology*.) An example of an unicellular plant.

Some cells are approximately spherical in shape; among these are certain eggs, and certain unicellular plants. In most cases, however, the form is modified by growth in special directions, or by pressure of surrounding cells or other structures. In size, cells are usually microscopic, the diameter of many of the human cells being as low as four one-thousandths (.004) of a millimeter (usually written 4μ ; read four micro millimeters, or four **mikrons**).⁴ Human red blood corpuscles are quite uniformly

² Schultze, *Arch. f. Anat. u. Physiol.*, 1861, S. 11.

³ Virchow, *Arch. f. Pathol. Anat.*, 1855, VIII, S. 27.

⁴ There is some confusion in regard to the term 'micro-millimeter'. Certain authors (mainly physiologists) use it to designate the one-thousandth part of a millimeter; other authors (mainly physicists) employ it to signify the one-millionth part of a millimeter. Conventionally, the prefix 'micro-', when it is the solitary prefix to the name of a unit of measurement, means the millionth part of that unit. One micro-volt, for example, is the one-millionth part of a volt. The use of 'micro-' before another prefix, as in 'micro-millimeter' is unfortunately not standardized.

The Greek letter corresponding to the initial of a standard of measurement always represents the one-thousandth part of the smallest common unit of that standard. Thus, μ (*mu*) indicates the thousandth part of a millimeter, and $\mu\mu$ (*mu-mu*) represents the

about 7.5μ in diameter. Cells of voluntary muscles, although but a few μ in diameter, may be several centimeters long. Human nerve cells may be as much as a meter in length, and in larger animals there are nerve cells of even greater length. The largest single cells are the yolks of birds' eggs; these cells do not contain more protoplasm than do microscopic cells,⁵ but they are swollen by the great amount of foreign material present.

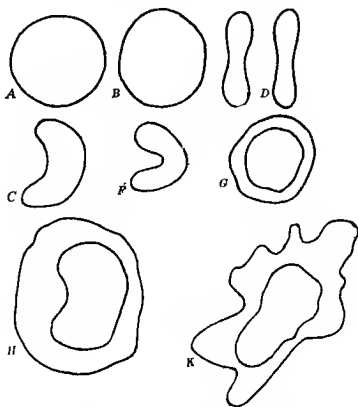


FIG. 3. Diagram showing the forms of certain of the blood corpuscles as enlarged 1200 diameters. *A, B*, largest outline of red blood corpuscles. *C, D, F*, cross section of red corpuscles, perpendicular to largest outline. Red corpuscles as prepared on microscope slides usually have the form corresponding to *D*, sometimes that corresponding to *C* or *F*. Histologists differ as to which is the normal form of the corpuscles in the blood vessels of the living animal. *G, H, K*, white corpuscles; *G*, lymphocyte; *H*, large mononuclear leucocyte at rest; *K*, the same in motion.

The protoplasm within the cell, exclusive of the nucleus, is called **cytoplasm**. Under examination, the cytoplasm is sometimes homogeneous in appearance, sometimes it appears to be finely granulated, and sometimes it appears to consist of a reticulated or meshed structure of fine threads, the **spongioplasm**, the meshes filled with a semi-fluid, the **cytolymph** or **hyaloplasm**. Some histologists hold that the typical structure of the cytoplasm is *alveolar*, that is, made up of globular droplets separated from

millionth part of a millimeter. Correspondingly, σ (*sigma*) indicates the thousandth part of a second, and γ (*gamma*) if used would represent the thousandth part of a milligram.

⁵ The protoplasm and nucleus contained in the yolk of a hen's egg is about 1% of the 'germinal disc' which is visible on one side of the yolk. A human egg is about 170μ in diameter.

one another by walls of a different substance; this is the arrangement of the particles of an emulsion.

The nucleus is a body which is in some cells approximately spherical, but which in other cells has a variety of shapes. It is made visible, as are the other details of cell structure, by 'staining' the tissue prior to examination under the microscope. The various dyes used darken different portions of the cell to different degrees. The nucleus, however, is usually visible without staining, because its refractive effect on light is not the same as that of the cytoplasm.

In addition to the nucleus and the cytoplasm proper, a cell usually contains certain other bodies. The most important of these are the **centrosomes**, which have a function in cell reproduction, and *plastids* which are concerned in the production of various organic compounds. Among the latter are the *amyloplastids*, or starch-producing bodies, and the *chloroplastids*, or chlorophyl-producing bodies, of certain plant cells. In addition, almost all cells contain foreign particles, *metaplasm*; these may be particles of food not yet assimilated, or pigment, or oil, or water, or waste products of cellular activity, etc.

Some cells, principally in plants, are each surrounded by a cell wall, which is produced by the cell. In animal cells, the outer layer of cytoplasm constitutes a *cell membrane*, which is not structurally distinguishable from the cytoplasm adjacent to it, but which nevertheless has certain functional peculiarities.

The nucleus is the controlling factor in the *metabolic* activity of the cell (the breaking-down of chemical combinations, *katabolism*, and the building-up of other combinations, *anabolism*), and upon it therefore depends the growth and the reproduction of cells, as well as their other vital functions. It is nevertheless true that certain cells, when deprived of their nuclei, may live for some time, and perform such functions as are generally ascribed to katabolic activity; may respond to stimulation by contraction, or by transmitting the stimulation to other cells, etc. Cells in which anabolic activity is especially important (gland cells), have significantly large nuclei, and the nuclear surface is sometimes rendered relatively large through the formation of branches or other irregularities of shape.

The nucleus, when a section of tissue is stained with certain dyes, is darker than the cytoplasm, and when examined under a high-power microscope is seen to have the dye absorbed principally by a certain portion, which is for this reason called **chromatin**. In addition to the chromatin, there is in the nucleus a small rounded body, the **nucleolus**, which also stains deeply, and a reticulum or network of fine fibers, the **linin**, the meshes of which are filled with *nuclear juice*. In some cells, the chro-

matin forms an independent, coarser, network, ramifying through the linin network ; in other cells the chromatin is in the form of granules distributed

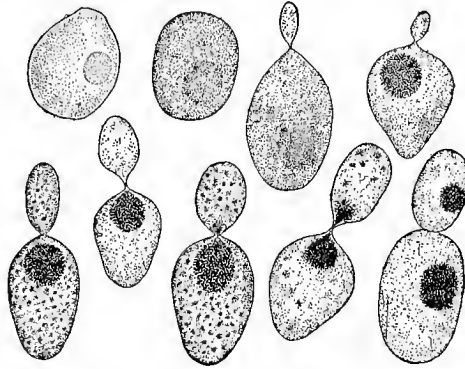


FIG. 4. Yeast cells budding. (Sedgwick and Wilson, *General Biology*.) The drawings of the successive stages, beginning at the left of the top row, show how the bud forms from the cytoplasm before the nucleus divides.

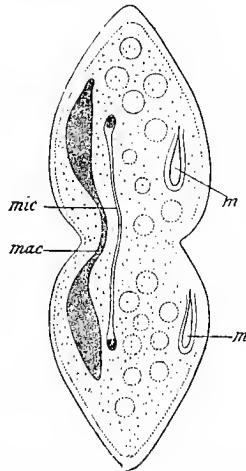


FIG. 5. Diagram of fission (Amitotic division) in the unicellular animal *paramecium*. (Sedgwick and Wilson, *General Biology*.) Paramecium belongs to the class *infusorium* which have nuclei differentiated into two distinct parts, *viz.*, a relatively large oval *macronucleus* and a much smaller *micronucleus* lying beside it. In the figure the division of the macronucleus (*mac*) and of the micronucleus (*mic*) is shown nearly completed, and division of the cytoplasm in progress. The paramecium has a definite mouth, shown at *m*.

along the linin fibers. The distribution of the chromatin is in all cases essentially modified during the process of mitotic cell division, as described below. Of the function of the nucleolus, practically nothing is known.

There are three characteristic ways in which new cells are produced by preëxisting ones. 1. **Budding.** [Fig. 4.] The new cell grows directly out of the old one as a twig grows out of a limb. In this case the parent cell apparently retains its identity, and we can speak of the new cell as

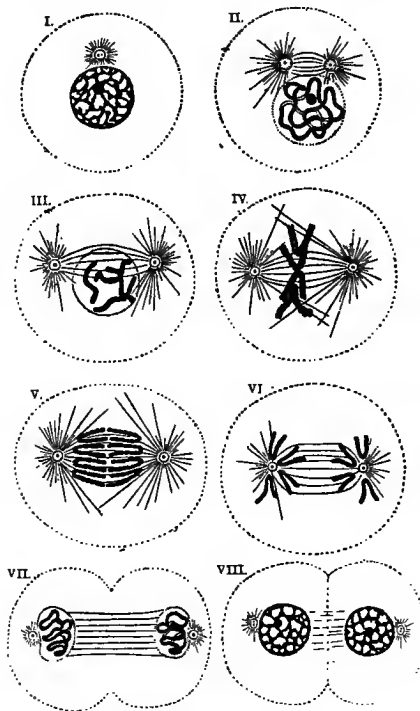


FIG. 6. Diagram of several successive stages in karyokinesis (mitotic division). (Schäfer, *Microscopic Anatomy*.) I. shows the 'resting' cell, i. e., the cell before the commencing of mitosis. VIII. shows mitosis virtually complete, the two new cells being in the 'resting' condition.

the daughter cell. The daughter cell is partially formed from the cytoplasm of the parent cell, and then a portion of the parent nucleus is separated from the remainder and passes into the daughter cell. 2. **Fission**, or *direct division* [Fig. 5]. The cytoplasm and the nucleus divide by progressive constriction, beginning in the nucleus so that two daughter cells are formed, half of the old nucleus going to each. 3. **Mitosis**, *indi-*

rect division or *karyokinesis* [Fig. 6]. This is the more usual form of cell division in multicellular organisms, and is rather complicated. In contrast with mitotic division the first two forms described above are called **amitotic**. Budding is never found in cells of the higher order of organisms, and fission occurs in these organisms only where the cells are pathological, or are approaching the end of their lines of descent from natural causes, as is the case with the cells of the membrane which lines the bladder, where the cells are constantly being lost from the surface and replaced by others formed below.

In **mitosis**, the nucleus takes up a position near the center of the cell, and the chromatin forms a relatively thick thread, usually continuous in the early stages of mitosis. This chromatin thread, the **skein** or **spireme**, divides longitudinally into two nearly equal threads, and each of these halves next breaks up into a number of short pieces which are called **chromosomes**. Meanwhile the centrosome, if not double at the beginning, has divided, and the two centrosomes have moved apart to positions on opposite sides of the nucleus. The linin network at the same time has been replaced by the **mitotic spindle** of fine lines spreading out in cone shape from the centrosomes and meeting midway between. (This is a typical order of events: in many cases the sequence is different. For example: the lateral division of the spireme may occur before the longitudinal division: or there may be no spireme formed.)

Eventually, half of the total number of chromosomes are drawn to each centrosome, where they unite to form a new skein, from which the chromatin is then distributed into its usual form in the new nucleus.

During the formation of the new nuclei the parent cell has begun to constrict about the equator defined by the polar axis through the two centrosomes. With the final completion of this constriction, the original parent cell is replaced by two daughter cells. The whole process of mitotic division may require from a few minutes to several hours.

The presence of a centrosome can not be demonstrated in all cells. In some cells, on the other hand, there are many centrosomes. It is possible that in amitotic division the centrosome plays an important part; and some investigators believe that it has an important rôle apart from its function in reproduction. Certain cells, such as spermatozoa, some unicellular plants and animals [Fig. 2], and the cells lining the respiratory passages, have fine **cilia**, projecting externally, which are capable of a whip-like motion. In some cells, it is quite clear that these are connected with centrosomes, and the analogy between the cilia and the lines of the mitotic spindle has suggested that the formation of such fibers is in every case the work of centrosomes.

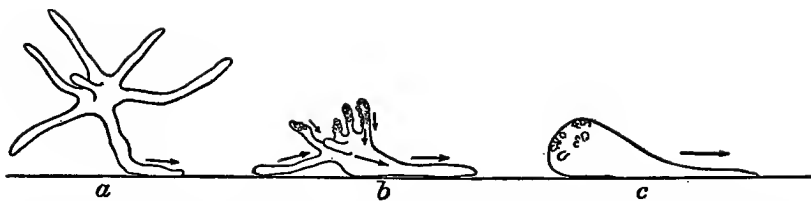


FIG. 7. Diagram showing an amoeba in three stages of locomotion. (Jennings, *Contributions to the Study of the Behavior of Lower Organisms*.) In *a* the amoeba, with its pseudopodia fully extended so that its body is reduced to little more than a pseudopodial conjuncture, is floating in the water, but one pseudopod has come in contact with the surface of a solid. In *b* the protoplasm has begun to flow out of the other pseudopodia into the one attached to the solid. In *c* the amoeba is reduced to a more compact mass, creeping along the surface. In thus creeping the protoplasm flows from the larger portion into the smaller, and the upper surface moves forward, so that the motion is somewhat like that of rolling a bag partly filled with a semi-fluid, by pulling on the front edge.

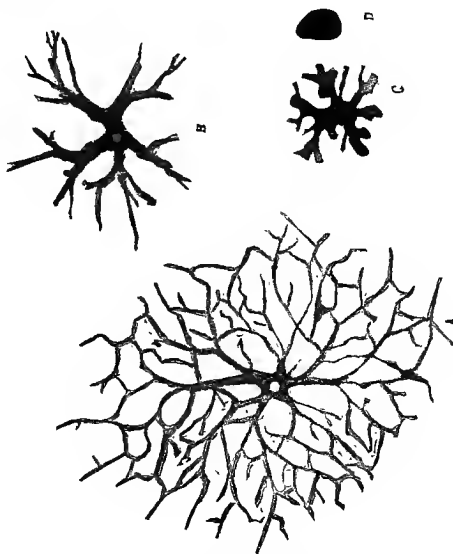


FIG. 8. Pigment cell from skin of frog, showing four stages, from A, complete extension, to D, complete retraction of the pigment. (Verworn, *Allgemeine Physiologie*.) It is a question whether the cell-branches are retracted and extended (and are therefore to be considered as pseudopodia) or the branches are fixed in form, and only the pigment moves.

Certain unicellular organisms are able to throw out **pseudopodia**, or leg-like projections of the protoplasm, and retract them, thus assuming

various irregular shapes [Fig. 8]. By means of these pseudopodia certain cells are enabled to move about; according to one theory, using them very much like legs; according to another theory, by a process which may be described briefly if not quite accurately), as "putting out a pseudopodium and then crawling into it." Cells which creep about in this way are called *wandering cells*, of which there are several sorts in the human body, among them the white blood corpuscles, or leucocytes [Fig. 3], and the osteoblasts [Fig. 15]. From the amoeba [Fig. 7], a typical unicellular animal found in pond-water, this method of locomotion is called **amoeboid movement**.

By means of pseudopodic projections of its cytoplasm a wandering cell may surround foreign particles, which if nutritive, may be assimilated within the cell, or if not, may be carried to another place and there deposited.

The activity of every living cell, and therefore of every living organism, is regarded as based chemically on the processes of *assimilation* and *dissimilation*. Assimilation is the conversion of food materials into new protoplasm; dissimilation is the breaking-down of protoplasm into waste products, and is usually accompanied by, or consists in part in, oxidization. Certain cells are able to carry on, in addition to assimilation proper, the synthesis of non-living substances to be stored up in the cell, such as fat, sugar, and starch, or to be cast out, as glandular secretion. Such synthesis, and assimilation likewise, is accompanied by the transformation of kinetic energy received from without (as from the sun's rays in the case of plants producing starch), or from dissimilation within the cell, into potential energy. Dissimilation liberates energy, which may be utilized in anabolic processes, or may be available as heat to maintain the temperature of the organism, or may be expended in work, as in the contraction of the muscle or the conduction of a stimulation in a nerve cell.

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CHAPTER II.

THE ADULT TISSUES OF THE HUMAN BODY.

FROM the fertilized human egg cell there develops a body composed of cells differing widely from one another in details of structure and function; together with certain non-cellular structures produced and nourished by cell activity.

The tissues of the body necessarily vary in structure with the stages in the development of the individual. We are concerned directly with the human tissues as they exist in the adult, but will find it profitable to refer briefly to their development within the uterus. Several classifications of tissue are in vogue, the one here adopted being taken from Stöhr.

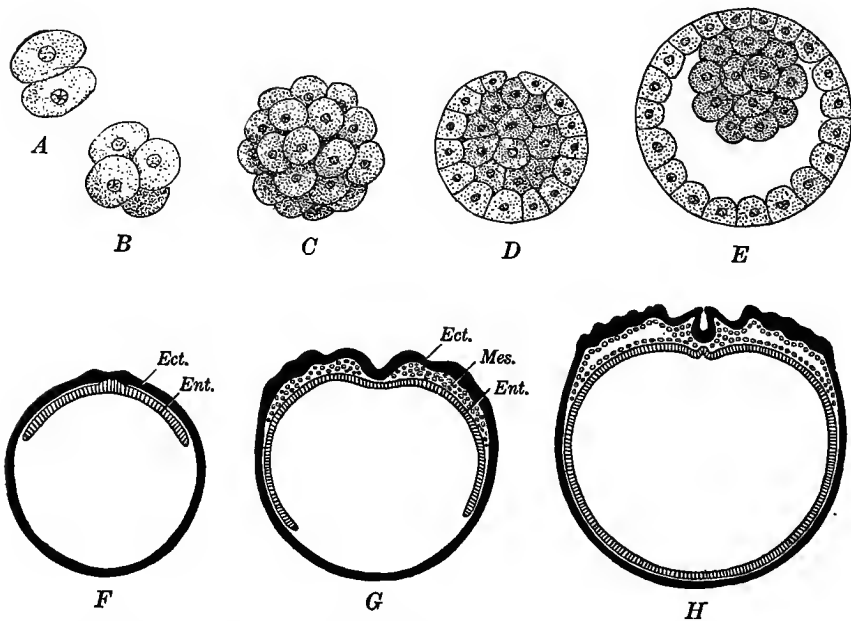


FIG. 9. Segmentation of the ovum (egg), and formation of the germ-layer in the rabbit. (Lewis & Stöhr, *Histology*.) A, two-cell stage; B, four-cell stage; C, morula. D-H, cross-sections of later stages. *Ect.*, ectoderm; *Ent.*, endoderm; *Mes.*, mesoderm. In G, the medullary or neural groove is plainly visible at the top, and in H, the edges of the groove are about to unite to form the medullary tube.

The egg cell is transformed by repeated mitosis into the **morula**, a spheroidal mass of cells uniform in appearance [Fig. 9, C]. From this compact mass is next developed the **blastula**, a hollow vesicle, the cells being distributed to form at first a wall of a single layer, and then by continued multiplication forming three layers; the **ectoderm** or outer layer, the **endoderm** or inner layer, and the **mesoderm** or middle layer.

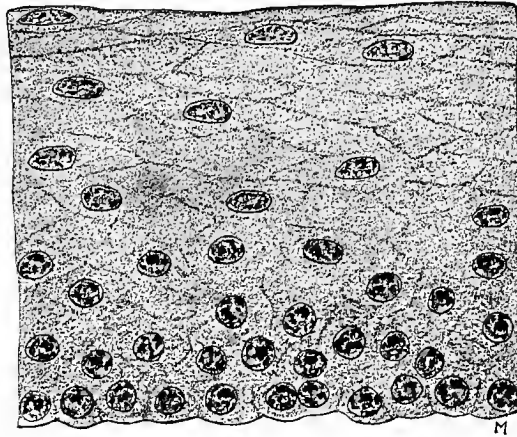


FIG. 10. Stratified epithelium from esophagus of cat. Highly magnified. (Bailey, *Histology*.)

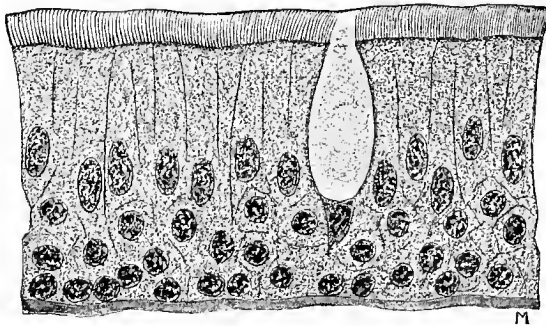


FIG. 11. Stratified ciliated epithelium from human trachea. Highly magnified. (Bailey, *Histology*.) The ciliated cells are columnar. One 'goblet cell' (cell secreting mucus) is shown.

The ectoderm and the endoderm are **epithelia**, composed of cells of compact form more or less closely arranged. The mesoderm is in part made up of cells like those of the two other layers, and in part of branch-

ing cells; **mesenchymal** cells; whose branches **anastomose**, that is, become joined together with protoplasmic continuity from cell to cell, forming what is called a **syncytium**.

From these three layers of the blastoderm develop the following tissues, comprising the body of the adult individual.

1. **Epithelium**. This is the tissue that covers surfaces, internal and external. The cells are closely packed, and cemented together by substances secreted by themselves. An epithelium may be **simple**, composed of one

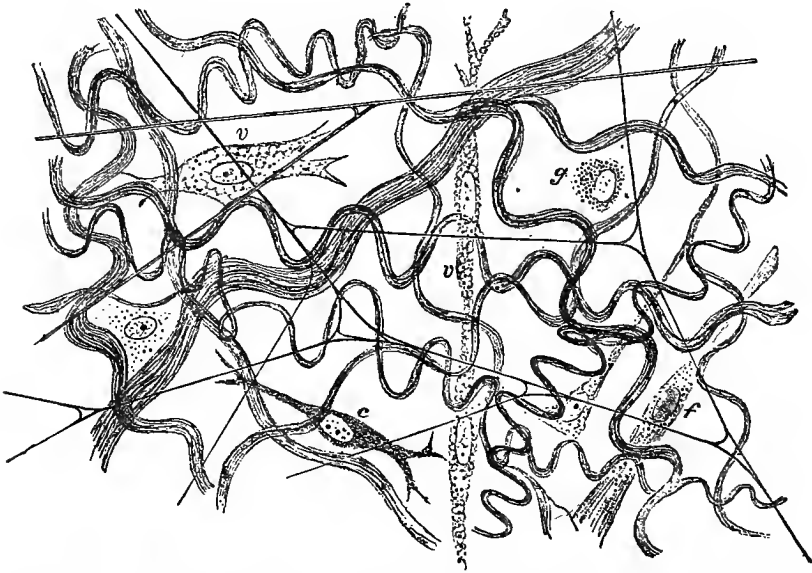


FIG. 12. Areolar connective tissue; sub-cutaneous, from rabbit. Highly magnified. (Schäfer, *Microscopic Anatomy*.) The wavy bundles are white fibers; the straight black lines forming an open net-work are elastic fibers. Several types of connective-tissue cells are shown at *e*, *f*, *g*, and *v*.

layer of cells; or **stratified**, composed of several layers [Fig. 10]. The cells from surface view are usually polygonal, and often six-sided. If the depth of the cells is approximately equal to their width, the epithelium and its component cells are both described as **cuboidal**; if the depth is greater than the width, they are called **columnar** [Fig. 11]; if the depth is less than the width, giving the cells a flattened or scale-like form, the term **squamous** is applied.

Epithelial cells may become hardened ('cornified'), as on the surface of the epidermis, on the nails, and in hair. Other epithelial cells may

have cilia projecting from the free surface, as in the lining of the bronchial tubes, the lining of the efferent ducts of the testes, and certain cells of the inner ear. Certain other cells are active secreting organs, such as the 'goblet cells' which secrete mucous.

The various epithelial tissues of the adult body develop from all three embryonic layers.

2. **Connective tissue.** This is derived from the mesenchymal cells of the mesoderm, and is typically composed of cells with intercellular spaces largely filled with substances secreted by the cells, notably **fibers** of two sorts, **white**, and **elastic**. In some connective tissues the bundles of fibers are closely packed and are generally parallel; in others (**areolar**⁶ and **reticular** connective tissues), the fibers are more loosely arranged, and run in various directions [Fig. 12].

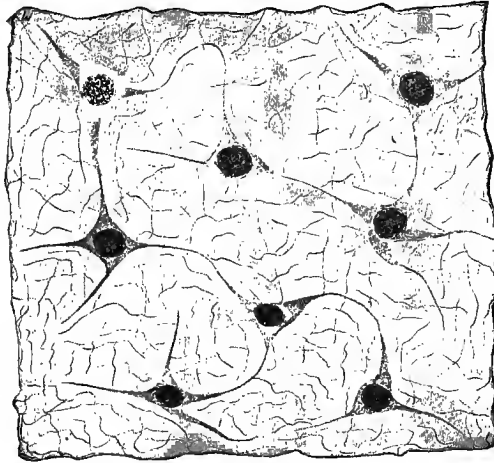


FIG. 13. Mucous connective tissues from umbilical cord (navel string) of eight-inch foetal pig. Magnified 600 diameters. (Bailey, *Histology*.) Fibers have begun to form in the 'ground substance' between the cells.

Some connective tissue has no well-developed fibers, the intercellular spaces being filled with gelatinous substance. This is **mucous tissue** [Fig. 13], and in it the cells show plainly the typical mesenchymal form.

⁶ *Areolar* means literally having spaces between the parts: hence loosely arranged. This word must be distinguished from *alveolar*, which means literally having cavities or cells (as honey-comb, for example). *Reticular* means having the form of a net, or network

When the cells of connective tissue become charged with fat globules, it is known as fat or **adipose** tissue [Fig. 14].

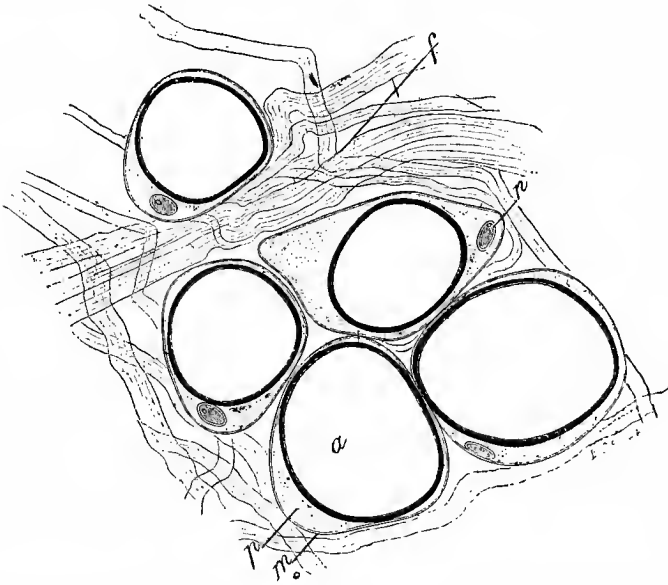


FIG. 14. Adipose sub-cutaneous tissue from dog. Magnified 200 diameters. (Ranvier, *Histologie*.) *a*, fat droplets; *p*, protoplasm; *m*, cell-membrane; *n*, nucleus.

Tendons, which connect muscles to bones, are dense strips of connective tissue with parallel fibers [Fig. 15]. The tendon as a whole is

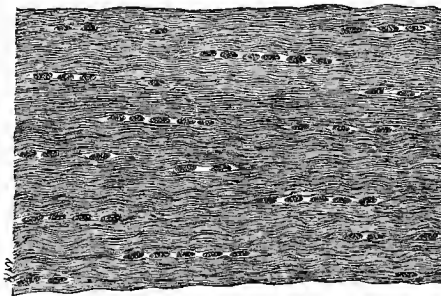


FIG. 15. Longitudinal section of tendon of frog. Magnified 250 diameters. (Bailey, *Histology*.) Rows of nuclei of tendon-cells are shown flattened between the fibers.

enclosed in a sheath of looser connective tissue, and the smaller bundles

of longitudinal fibers within the tendon are also enclosed in sheaths of connective tissue continuous with that of the larger sheath.

Wherever the connective tissue fibers are found, the cells which nourish

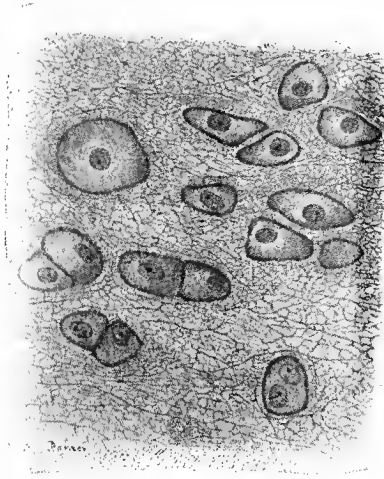


FIG. 16. Elastic cartilage (gristle) from human ear. Magnified about 290 diameters. (Szymonowicz, *Histologie*.) Showing cartilage-cells, and elastic fibers.

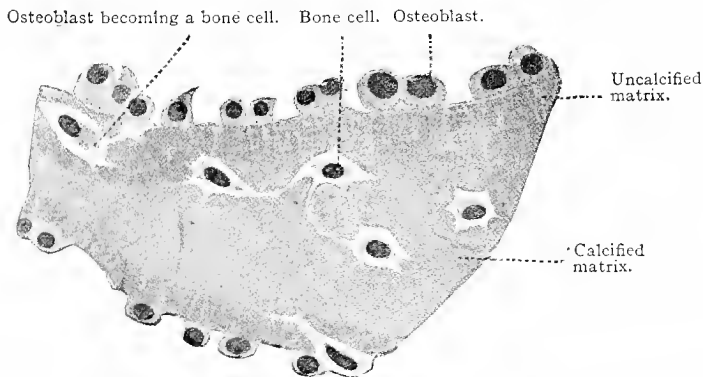


FIG. 17. Part of a cross-section of a bone from a four-month human embryo. Magnified 675 diameters. (Lewis and Stöhr, *Histology*.)

them are found also. In the dense tissues the cytoplasm and nucleus may be flattened between fibers or in thin plates wrapped around them.

3. **Bone** and **cartilage** are produced by mesenchymal cells. Bone is deposited by a specialized cell, the **osteoblast**, which as it encloses itself

within the bone it manufactures, is called a **bone cell** [Fig. 17]. Cartilage is formed as the thick cell walls secreted by the **cartilage cells** [Fig. 16].

4. **Nerve tissue** comprises the 'nerves', spinal cord, brain, and other ganglia, and is derived wholly from the ectoderm.

5. **Muscle.** **Smooth** or *non-voluntary muscle* develops from the mesenchymal cells of the mesoderm. **Striped** or *voluntary muscle* develops from the non-mesenchymal cells of the mesoderm.

6. **Vascular tissue.** This includes the blood and lymph, the lymph glands and the red marrow of the bones, and develops from the endoderm.

7. **Glands.** The active tissues in these are composed of modified epithelial cells. Glands are developed from all three blastodermic layers.

Nervous, muscular, and glandular tissues will be treated more fully in the following chapters.

REFERENCES ON TISSUES GENERALLY.

Schäfer, *Microscopic Anatomy*, § Structure of the Tissues, Sub-§§ The Elementary Tissues, The Epithelial Tissues, Connective Tissue.

Bailey, *Histology*, Part III, Chapters I-III.

Lewis and Stöhr, *Histology*, Pt. I, § II, Sub-§§ Histogenesis, Epithelium, Mesenchymal Tissue.

Hertwig, *Manual of Zoology*, § General Anatomy, II.

CHAPTER III.

MUSCULAR TISSUE.

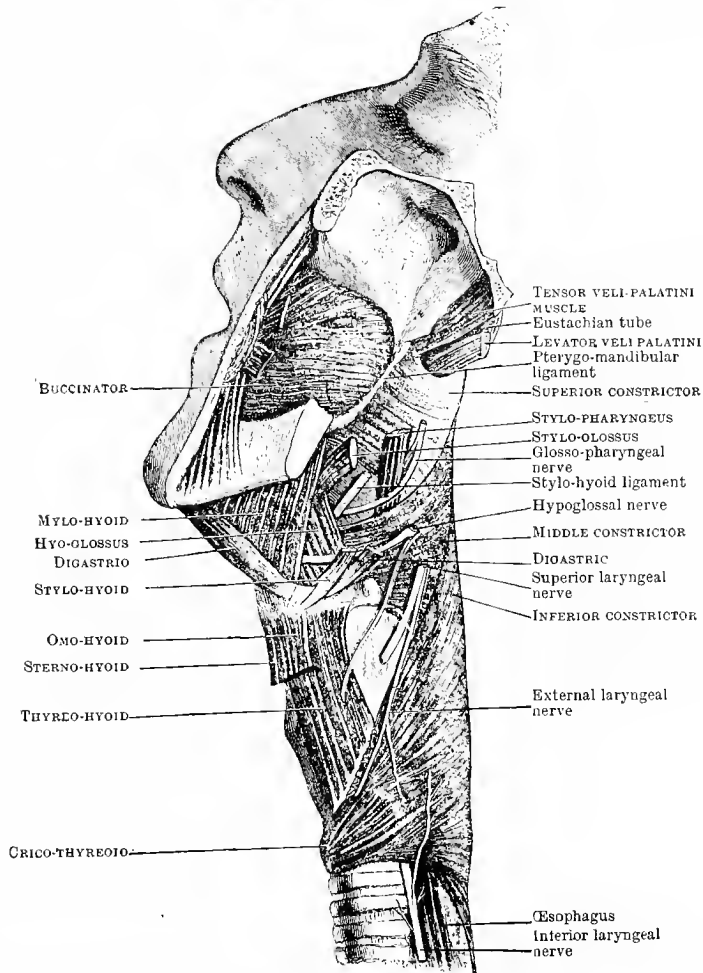


FIG. 18. Lateral view of the wall of the pharynx, showing some of the muscles involved in vocalization. (Cunningham, *Anatomy*.) The names of the muscles are in small capitals.

The muscles of the human body are usually classified under three heads.

1. **Striated** (striped) or 'voluntary'.
2. **Non-striated** (non-striped), **smooth**, or 'non-voluntary'.
3. **Cardiac** (heart-muscle), striped, but non-voluntary.

Striated muscle tissue forms the skeletal muscles, that is, the muscles of the body wall and of the limbs; and also the muscles of the eye and ear,

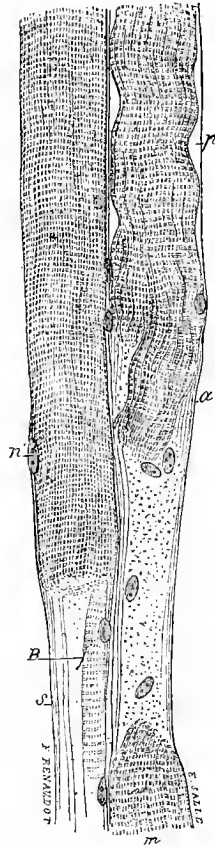


FIG. 19. Parts of two striped muscle fibers of dog. Magnified 270 diameters. (Ranvier, *Histologie*.) The fibers have been broken without breaking the sarcolemma. *n*, nucleus; *s*, sarcolemma; *p*, fluid between sarcolemma and muscle-cell.

the diaphragm, the tongue, pharynx, larynx, upper part of the esophagus, and in part of the rectum and genital organs.

Striated muscles develop from certain of the non-mesenchymal cells of the mesoderm. These cells, which are called **myoblasts**, divide by re-

peated mitosis and become elongated, and then shift to the positions corresponding to those which are to be occupied by the muscles in the mature body. The mesenchymal cells adjacent to the muscles form tendons and muscle sheaths and the *fascia* (broad sheets of connective tissue lying between the muscles and the skin).

The myoblasts consist of granular cytoplasm, called **sarcoplasm**, having fibrils near the periphery and centrally located nuclei, and are enclosed in a delicate connective tissue membrane, the **sarcolemma**. The myoblasts may have a diameter of from 10μ to 100μ .

The fibrils within the myoblast divide longitudinally, and group themselves, forming **muscle columns** $.3\mu$ to $.5\mu$ in diameter, between which lies the sarcoplasm.

The nucleus of each myoblast divides amitotically into many nuclei, which scatter along the cell, which has now become a **muscle fiber** [Fig. 19], a single cell which may be from 50 to 120 mm. in length, and from 10μ to 50μ in diameter.

In *pale* or *white* muscle the columns of fibrils nearly fill the fiber, with thin layers of sarcoplasm between them, and the nuclei are generally flat-

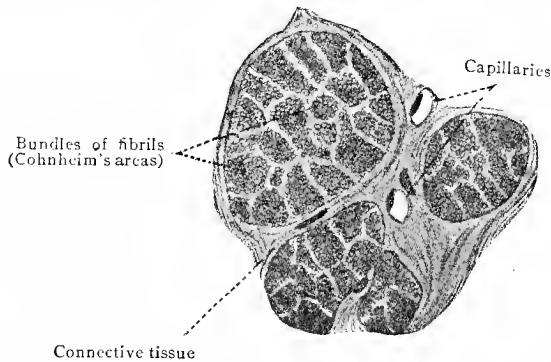
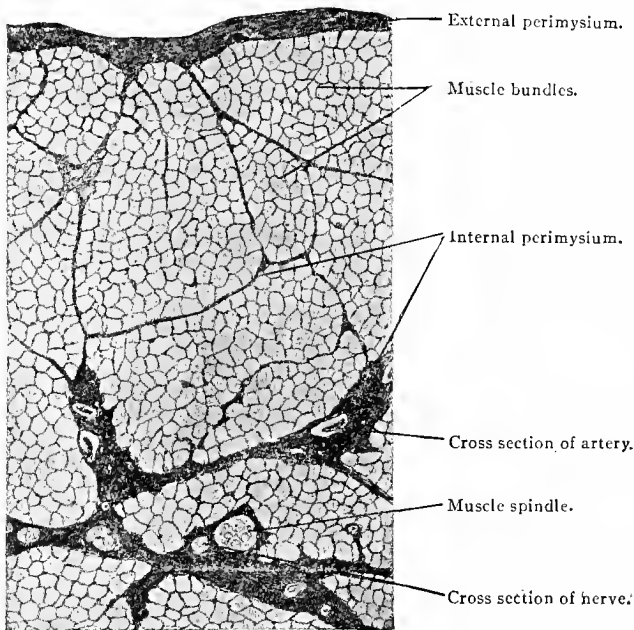


FIG. 20. Cross-section of four fibers of human *vocalis* muscle, showing the grouping of the myofibrils to form Cohnheim's areas. Magnified 590 diameters. (Lewis and Stöhr, *Histology*.)

tened in between the sarcolemma and the fiber. A few nuclei are found lying inside, among the bundles of fibrils towards the end of the fiber, and particularly towards the distal end, at which point elongation in growth takes place. In *dark*, or *red* muscle, there are fewer fibrils and more sarcoplasm, and the nuclei are located more centrally, embedded among the fibrils. Connective tissue, including cells with indefinite out-

lines and flattened nuclei smaller than the nuclei of the muscle fibers, not only surrounds each fiber, but surrounds small bundles of the fibers, bundles of these bundles, and the whole muscle. In cross section this connective tissue forms a continuous network, enveloping and reticulating within the muscle [Fig. 20].

The sheath of the whole muscle is the **external perimysium**, the connective tissue within the muscle is the **internal perimysium** [Fig. 21]. Lymph and blood vessels and nerves are found in the internal perimysium. The nerve terminals are either on the surface of the ordinary muscle fibers, or on fibers enclosed in muscle spindles.



MUSCLE OF MAN. $\times 60$.

FIG. 21. Cross-section of human striped muscle (*omohyoid*), magnified 60 diameters. (Lewis and Stöhr, *Histology*.)

The individual fibrils are composed of two kinds of substance, arranged in regular alternation. The **isotropic** substance singly refracts light, and does not readily stain in the preparation of sections. The **anisotropic** substance is doubly refractive, and stains deeply. The arrangement of these two substances in the fibrils of a single cell is practically parallel, and this gives the 'striped' appearance to the fibers. The functions of

these two substances is not understood, but there are several tentative theories as to the way in which they behave in the process of contraction.

The muscle fibers are rounded or conical, the end towards the tendon being more obtuse than the other. Connection with the tendon is provided by the perimysium, which is continuous with the tendon [Fig. 22]. The connection of a muscle with a tendon, or with other tissues, at its relatively moveable end, is called its **insertion**; the attachment at the relatively fixed end of the muscle is its **origin**. In the cases of muscles inserted in the skin, or the mucous membrane, the ends of the fibers may be branched or pointed, the perimysium being prolonged as elastic fibers which become continuous with the connective tissue in the skin or membrane.

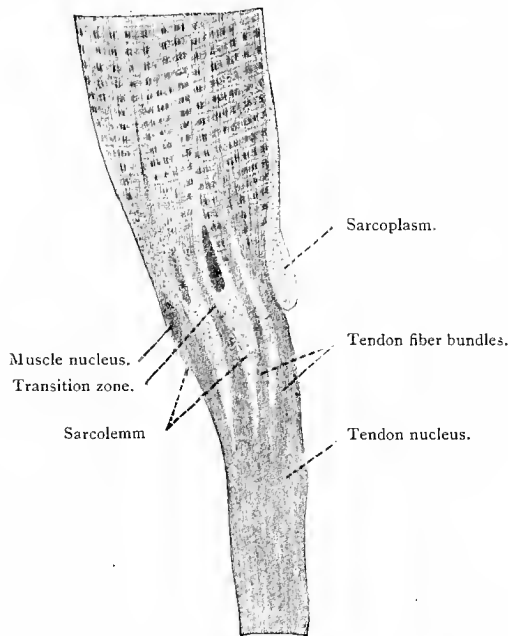


FIG. 22. Junction of striped muscle and tendon in frog. Magnified 750 diameters. (Bailey, *Histology*, after Stöhr.)

Smooth muscle develops from mesenchymal cells. It is found surrounding the large blood vessels and lymphatic ducts, the intestinal canal and the ducts of the principal gland opening into it, the large respiratory tubes and the passages and ducts of the genito-urinary system, and subcutaneously in connection with hairs. It may for convenience (although not with exact accuracy) be called **visceral** muscle, in contradistinction to skeletal muscle.

The fibers of smooth muscle are elongated spindle-shaped cells, each with a single nucleus centrally located [Fig. 24]. The fibers vary in length from 20μ to 500μ and are typically about 5μ in diameter. Within these cells 'coarse' longitudinal fibers, composed entirely of anisotropic

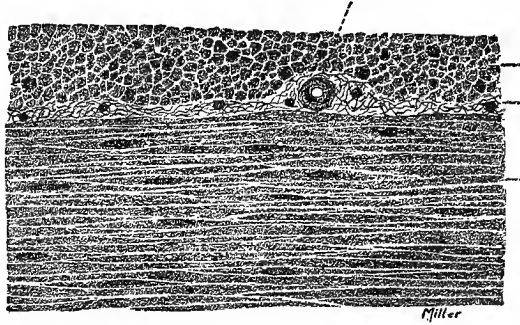


FIG. 23. Smooth muscle in longitudinal section of small intestine. Magnified 350 diameters. (Bailey, *Histology*.) The inner circular layer (at top), traversely cut, and the outer longitudinal layer are shown with the intermuscular septum of connective tissue between. The cross-section of a small artery is visible in the septum.

(i. e., doubly refracting), substance develop near the surface. These *border fibrils* are believed to be continuous from cell to cell. Surrounded by the border fibrils are fine *inner fibrils*, which separate to pass around the centrally located nucleus. Smooth muscle fibers are covered by con-



FIG. 24. Isolated smooth muscle cells from human small intestine. Magnified 400 diameters. (Bailey, *Histology*.) The centrally located nuclei are visible as oval, darker areas.

nective tissue in much the same way as are the striped muscles, except that two or more cells in longitudinal contiguity may be enveloped in the same sheath.

The muscle of the vertebrate heart belongs to the type designated as **cardiac**. The fibrils of cardiac muscle are composed of alternated sections of isotropic and anisotropic substances, but the cells have usually a single centrally located nucleus, like the smooth muscle cell. According to some observers, the cardiac muscle does not consist of individual cells, but is a **syncytium**, that is, a tissue in which there is protoplasmic continuity

from cell to cell, so that the limits of the individual cells can not be exactly assigned. This **anastomosis** (union of cells) is not confined to the longitudinal direction, but occurs between lateral surfaces also of contiguously lying cells, so that heart muscle, according to this view is "a network of broad protoplasmic bands, in and near the centers of which nuclei are situated at irregular intervals" (Stöhr) [Fig. 25]. According to other

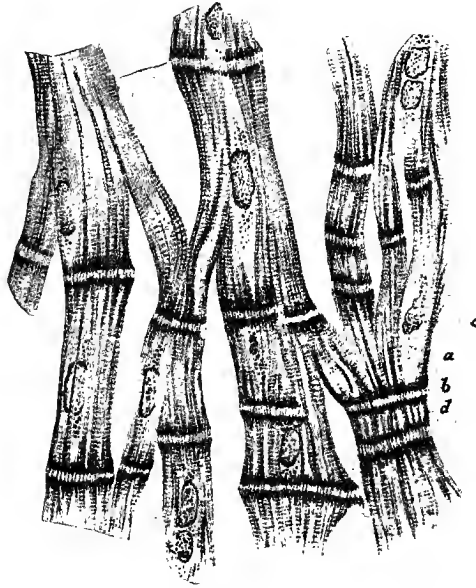


FIG. 25. Muscle fibers of heart, showing syncytial structure. Highly magnified. (Schäfer, *Microscopic Anatomy*, after Przewoski.) *a*, septum; *b*, fibrils bridging septum; *c*, nucleus; *d*, short segment without nucleus.

observers, there is merely longitudinal continuity of fibrils, not of protoplasm, the apparent anastomosis being produced in the process of preparing the section of tissue for observation. The groups of mesenchymal cells from which smooth and cardiac muscles develop, do, however, show well-marked anastomosis between their branches.

Mesenchymal cells, in becoming cardiac muscle cells, lose their original power of reproduction. Possibly striated muscle can reproduce.

THE FUNCTION OF MUSCLE.

The most important characteristic of the muscle cell is its highly-developed power of contraction. Many other cells are able to contract, or to change their shape in various ways; but in the muscle cell, contractile

function is developed to the highest degree. The beating of the heart, the regulation of the diameters of blood vessels, the inflation of the lungs, the movement of food along the alimentary canal, the erection of the body hairs in 'gooseflesh', the movements of the limbs and other portions of the body, are produced by the properly timed contractions of myriads of muscle cells.

In contracting, the muscle cells become thicker and shorter, and undergo internal changes which are not well understood. During this process, toxic substances, having decided effects on both muscular and nervous tissue, are formed. In its resting phase the cell carries on metabolic processes which maintain its own life, produces material essential to the process of contraction, and possibly produces substances of value to other tissues.

Under ordinary circumstances a striated muscle contracts only when it is **stimulated** by some external agency. Normally, the stimulation is an impulse conveyed to the muscle fiber from a ganglion cell through its axon, whose terminal branches are in contact with the sarcoplasm beneath the sarcolemma. Contraction can be produced, however, by mechanical, electrical, chemical, or thermal stimuli applied directly to the muscle. A muscle from the leg of a frog, for example, contracts if pinched by a pair of tweezers, or if an electric current be made or broken through it, or if ammonia or certain salt solutions be applied to it. If the muscle be gradually warmed, it commences to contract at about 34° C. (93° F.), the contraction increasing up to about 45° C. (113° F.), at which point the muscle dies, although the contraction lasts some time longer as *rigor caloris*.

When a single stimulation is applied to a striated muscle there is a brief **latent period** after the stimulus, and then the muscle responds with a single short sharp contraction, relaxing immediately. The duration of the latent period, contraction and relaxing vary with the intensity of the stimulus, and with the temperature, **tonus**, (tone; *vide infra*, VIII), and fatigue of the muscle, and with the work done. The frog's gastrocnemius muscle, at ordinary room temperature may, when excited by an induction coil current, give such results as: latent period, 10σ; contraction, 40σ relaxing, 50σ; the whole process therefore taking place within $\frac{1}{10}$ sec. (1 second is 1000σ). In the living animal, when the muscle has tone, the times may be much shorter.

The amount of shortening which a striated muscle displays is influenced by the same conditions which control the time relations of the process. Under similar conditions of temperature, fatigue, etc., a weak stimulus may cause a slight contraction, a stronger stimulus a more pronounced contraction. There is, of course, a maximum for each muscle.

The same muscle under otherwise similar conditions, will contract less, if the 'load' or work done be greater. In the excised frog's muscle, the upper end may be rigidly supported, and a weight attached to the lower end. The extent of contraction will then decrease with increasing 'load'. If both ends be rigidly fastened, we may produce 'contraction' without shortening; the muscle being under longitudinal tension during the moment of activity.

When stimulated by ordinary means, the whole muscle fiber does not contract simultaneously. Contraction begins at the point at which the stimulus (whether nerve current or artificial stimulus) is applied, and spreads in both directions. The rate of propagation of the contraction is 3 to 4 meters per second in the frog's muscle, and may be as high as 6 meters per second in muscles of warm-blooded animals. The contraction is strictly limited to the fibers stimulated; and does not directly affect adjacent fibers. The contraction of a fiber may, however, cause contraction of other fibers in contact with branches of the same nerve axon, the stimulation of one branch by the contraction of the muscle fiber in contact with it being transmitted to the other branches and from them to the fibers.

When successive stimulations are applied to a muscle at such rate (15 to 40 per second, according to conditions), that before the contraction produced by one has ceased, another has occurred, the result is a single contraction, maintained as long as the stimulations continue, and much greater in extent than the contraction which would be produced by a single stimulus of the series. Such a state of contraction is called *tetanus*. If the stimuli are applied at a rate too slow to produce tetanus, but so that the successive stimuli arrive before the effect of the preceding one has completely disappeared (*i. e.*, before the end of the period of relaxing), the result is a series of contractions much greater in extent than the contraction resulting from a single stimulus of the same sort. This condition is called *summation of contractions*. Again, stimuli so weak that singly they produce no contraction, may, when given at a sufficiently rapid rate, produce contraction. This condition is known as the *summation of stimuli*. It is supposed that the 'voluntary' contraction of muscle is tetanic, due to a rapid succession of nervous discharges. There is some evidence that these discharges to the muscle occur at a rate of 40 per second.

The only continuous stimuli are those of the normal nerve activity, heat, and chemical action. Electric currents are effective only at the moment of making or breaking the current. Mechanical pressure is effective only at the moment when the pressure is increased or decreased.

TONUS AND EXCITABILITY.

The constant stimulation which is supplied by the nerves in the normal body keeps the muscles in a state of normal contraction (**tonus**), the degree varying continuously with the changes in the flux of nervous current. This continuous stimulation also heightens the sensitivity of the muscle to the more pronounced and definitely directed currents which bring about the coördinated contractions which produce movements; or in other words, increases the **irritability** or excitability of the muscle. If the efferent nerves supplying any of the muscles be severed, the muscles relax completely and become motionless, except in so far as artificial stimulation (*e. g.*, electrical) may be employed upon them.

In the case of cardiac and smooth muscle, and probably also in the case of striped muscle, certain nerve currents have an action which is **inhibitory**, *i. e.*, the reverse of excitatory. Certain nerve fibers, as for example the fibers of the vagus which supply the heart have inhibitory action only. Whether in all cases inhibitory currents are carried by special inhibitory fibers, or whether both excitatory and inhibitory currents may be carried by certain fibers, is unknown.

The factors upon which the irritability of muscle depends, are (in addition to stimulation and tonus of nervous origin), temperature, condition of rest or fatigue, and activity of various adventitious chemical substances. The greater the fatigue, the less the excitability. Salts of sodium increase the excitability, and calcium salts lower it. By immersing a thin striated muscle (*e. g.*, the sartorius of the frog), in a solution of NaCl 0.5%, Na_2HPO_4 0.2%, and Na_2CO_3 0.04% ("Biedermann's fluid"),⁷ it is thrown into a state of excitability which shows a certain likeness to that of smooth and cardiac muscle. The muscle, in this solution, contracts repeatedly, and may 'beat' rhythmically like heart muscle, but at a more rapid rate.

THE CONTRACTION OF CARDIAC MUSCLE.

Cardiac muscle, in its normal condition, like striated muscle in Biedermann's solution, contracts periodically without a periodic stimulus. The heart of a living animal receives excitatory currents from nerves of the 'sympathetic' system, and inhibitory currents from the vagus nerve; but these do not cause the periodic activity of the heart muscle. In reptiles and many other animals, the heart continues its contractions after being completely isolated from the nervous system, and even after being removed from the body. If the excitability of the excised heart be increased

⁷ Formula given by Starling, *Physiology*, page 235.

by immersing it in Biedermann's solution or one of certain other saline solutions, the beating may be prolonged for hours.

The stimulus producing the contraction is, in the case of the excised heart, internal; such can be considered to be the case in the undetached living heart. The nerve currents serve but to increase (or decrease) the excitability of the cardiac muscle, and hence to accelerate (or retard) the spontaneous activity. Chemicals which modify the excitability of the excised heart also modify the excitability of the heart *in situ*. Cardiac muscle, in addition to its power of periodic contraction without periodic stimulation from outside, and even without any external stimulation, responds to a single external stimulus by a single twitch, as does striated muscle. The contraction of the heart muscle so brought about differs from the corresponding contraction of striated muscle in three particulars: (1) The excitation may pass from fiber to fiber directly, because of the protoplasmic connections between fibers; (2) The degree of contraction is not dependent upon the intensity of the stimulus. If a fiber contracts at all it contracts with the full force of which it is capable. A stimulus which will not produce full contractions will produce no contractions at all; (3) Summation of contraction and tetanus do not occur in the case of the cardiac muscle. While the muscle is contracting, a stimulus has no effect on it. After the contraction, it becomes again irritable. The interval during which the muscle is unexcitable is called the *refractory period*.

THE CONTRACTION OF SMOOTH MUSCLE.

Smooth muscle resembles cardiac muscle in having active power of its own. Cut off from all nervous connection, it still may contract and relax alternately if subjected to a continuous external stimulus, *tension*, for example. In general smooth muscle responds to all the artificial stimuli to which striated muscle responds, and it also responds to various drugs, such as digitalis, ergot, salts of barium, etc., which produce different effects on smooth muscle of different organs.

Smooth muscle is supplied, like cardiac muscle, with a double set of nerves, one heightening the excitability and the other depressing it.

THE CHEMICAL PROCESS IN MUSCLE.

The chief products of muscular activity are carbon dioxid, water, and sarcolactic acid. Sarcolactic acid is isomeric with the lactic acid of sour milk, but the former rotates the plane of polarization of polarized light to the right, whereas the latter does not rotate the plane at all. It is probable that the primary chemical activity which conditions muscular contraction is the breaking-down of some complex substances, which may be

highly unstable, although one physiologist supposes it to be grape sugar ($C_6H_{12}O_6$). The lactic acid ($C_3H_6O_3$) is then oxidized, the oxygen being supplied by the red blood corpuscles. Oxidization is at any rate an important part of the chemical process in muscle, and through it is liberated the heat, or at least a part of the heat, which is a noticeable consequence of muscular activity.

Normally, the greater part of the lactic acid produced is oxidized in the muscle. If sufficient oxygen is not present the acid is thrown in abnormal quantity into the circulation, and excreted by the kidneys. In normal urine, from 3 to 4 milligrams of acid per hour are excreted. In one case, the urine passed thirty minutes after running a third of a mile contained 454 mgs. of lactic acid.

In the intervals of 'rest' the muscle cell builds up the complex substance which is broken down in the period of 'activity'. According to some physiologists the food material and oxygen are together built up into an unstable compound, which is broken down in activity, forming CO_2 , without additional oxygen. According to this theory, the account given above is erroneous.

FATIGUE.

If a muscle be repeatedly stimulated, its contractions eventually become less in extent, and the latent periods, as well as the periods of contraction and relaxation—especially the latter—become prolonged. In the human being this condition is accompanied by the experience of fatigue.

Whatever may be the exact nature of the chemical processes in muscular activity, it is probable that two factors contribute to fatigue: (1) the partial exhaustion of the stored material which the cell has elaborated as material for its contractile activity; (2) the accumulation of the products of decomposition. These substances (lactic acid, carbon dioxid, etc.) have an inhibitory or deadening effect on the muscle cell, and possibly some of them affect the sensory nerve endings in the muscles, producing the experience of fatigue. In the body the circulation of blood both brings fresh food material, to be built up into new muscle material, and also removes the waste products. If the muscle activity is relatively great, however, the waste product cannot be removed as fast as formed, and either the food material is not brought fast enough, or else the muscle cell cannot fast enough build up muscle material out of it.

THE ELECTRICAL PROPERTIES OF MUSCLE.

Under certain conditions an electric current may be drawn off from a muscle by applying suitable electrodes to it. If one electrode (A) is applied to an uninjured portion of a resting muscle, and the other (B) to a

cut or otherwise injured portion, a delicate galvanometer in circuit with A and B will show a very small current flowing from A to B. This is spoken of as the 'current of demarcation' or 'resting current'.

If electrodes are applied to an uninjured muscle, at some distance from each other, and the muscle is caused to contract, a current flows during contraction from the electrode at which the degree of contraction is lowest to the electrode at which it is highest. If, therefore, the muscle be stimulated at a point M, near one end, the electrode A being applied at the middle of the muscle and the electrode B at the other end, when the excitation wave reaches A, the current will flow from B to A, and when the wave reaches B, the current will flow in the reverse direction. This current is known as the 'current of action' or 'action current'.

The currents for muscle may not be of any special significance. They are in any case probably artifactual, that is, there is probably no *current* unless electrodes are applied and an external circuit established through them. In the case of the 'resting current' there may not even be a difference of potential between the cut and uninjured portions before the electrodes are applied.

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NERVOUS TISSUE.

SoP PS SG GC SB NC CC SC EC } SoP
 SpP }
 C
 SpM
 EN
 IMC N PA

FIG. 27. Transverse section of ferret embryo of greater age than shown in Fig. 26, showing medullary canal. (Cunningham, *Anatomy*.) NC, neural crest. CC, central canal. SG, spinal ganglia.

degree, but more uniformly, forming the **spinal cord**, with a small **central canal**.

As the medullary tube forms, some cells pass outwardly from the posterior portion forming the **spinal ganglia** (to be described later). At an early period, not definitely determined, other cells migrate from the growing spinal cord (or possibly from the spinal ganglia), forming the **sym-**

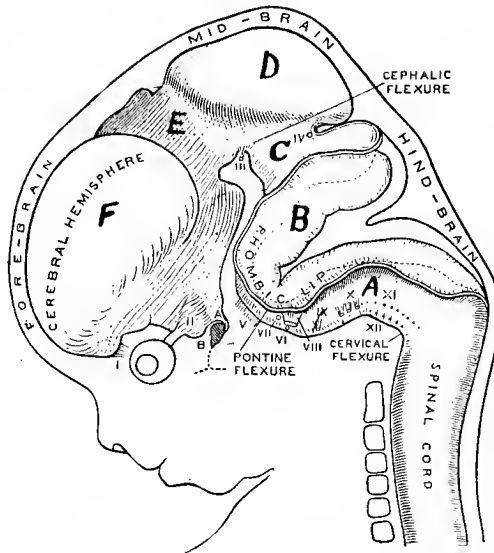


FIG. 28. Profile view of the brain of a human embryo of six weeks. (Modified from Cunningham, after His.) *A*, myelencephalon. *B*, metencephalon. *C*, isthmus. *D*, mesencephalon. *E*, diencephalon. *F*, telencephalon.

pathetic ganglia, and other **visceral ganglia**, more remote from the cord than are the spinal ganglia. From the anterior part of the medullary tube cells also migrate to the structures which become the cochlea of the ear, and the retina of the eye, and possibly to the sensory surfaces of the organs of smell and taste.⁸

From the brain, spinal cord, spinal ganglia, and visceral ganglia the nerve cells send processes (**nerve fibers**) to the various tissues of the body.

⁸ It has been a question whether the four autonomic or visceral ganglia in the head are formed by the migration of cells from the anterior part of the medullary tube, or from the sympathetic ganglia of the trunk. Recent investigations point to formation from both sources.

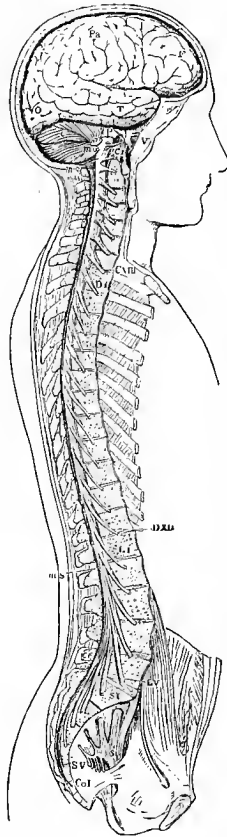


FIG. 29. Cerebro-spinal axis, reduced to $\frac{1}{8}$ diameter. (After Bougery.) A longitudinal section through the median plane of the spinal column, and in part of the skull; leaving in relief the brain, cord and spinal nerve-roots. Lobes of the cerebrum: *Pa*, parietal; *F*, frontal; *O*, occipital; *T*, temporal [compare Fig. 65]; *C*, cerebellum; *mo*, medulla oblongata; *Ct-Cviii*, cervical nerves; *Dt-Dxii*, thoracic nerves (formerly known as dorsal nerves); *Lt-Lv*, lumbar nerves; *St-Sv*, sacral nerves; *Co*, coccygeal nerve; *ms, ms*, upper and lower extremities of the spinal cord.

THE NEURON.

The essential elements of the nervous system are the nerve cells with their prolongations (**fibers**). The nerve cell, exclusive of the prolongations, is called the **cell-body**. The nucleus lies within the cell-body. The cell-body and the prolongations together are known as the **neuron**. There are two general kinds of fibers, designated **axon** and **dendrite** (or **dendron**), whose differences will be described later.

The chief function of the neuron (aside from nourishing itself) is *conduction*. So far as is now known, the importance of the neuron for the total organism is the fact that it can receive stimulation from (can be irritated by) another neuron or by an extra-neural agency; and can transmit this stimulation through itself to another neuron, or to a muscle or gland.

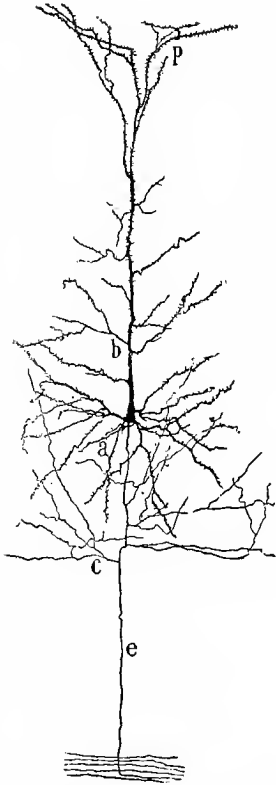


FIG. 30. Nerve cell from the cerebral cortex. Magnified. (Ramon y Cajal.) *e*, axon. *c*, collaterals of axon. *a*, *b*, dendrites (dendrons). *P*, teleodendrites, or terminal branches of principal dendrite.

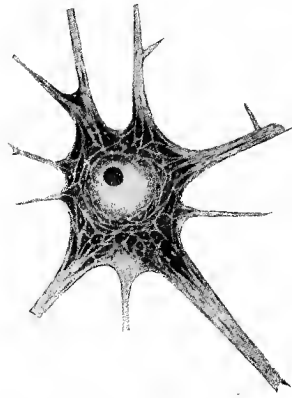


FIG. 31. Motor cell from ventral horn of gray matter of rabbit's spinal cord. Highly magnified. (Barker, *Nervous System*, after Nissl.) The process (fiber) extending directly downwards is the axon; the others are dendrites.

Beyond this activity (and self-nourishment) we have no evidence of any other important function of the nerve cell. In its development the power of conduction, which is possessed by less-highly specialized cells (and even by muscle cells which are specialized in a different direction) has reached

the highest degree of efficiency. Coincidentally, the nerve cell has lost the power of contraction, and like muscle and other highly-specialized cells, the power of reproduction.

A neuron as a whole can conduct in but one direction. It receives impulses through the dendrites (of which there may be several) and sends them out through the axon (each cell having one axon).

Taking the cell-body as a center of reference, we may say that the dendrites conduct *in*, and the axon conducts *out*. The only possible difference in conduction between fibers (*i. e.*, axon and dendrites) and the cell-body, lies, however, in the fact that the 'current' or 'discharge' may become intensified in passing through the cell-body.



FIG. 32. Synaptic connections of axon-branches with cell-bodies in the cerebellum. Highly magnified. (Ramon y Cajal.) *b, c*, axon of cell *B*, with branches in contact with 'cells of Purkinje' in row at right of *A*.

As to the nature of the nerve current, *i. e.*, what passes when the neuron is irritated at one end, and shortly thereafter at its other end irritates another neuron or a gland or muscle cell, we can merely guess. Probably it is a chemical process, analogous to the action in a train of powder, which, when lighted at one end, carries the combustion process to the other end.

It is customary to classify the neurons as (1) *sensory*, (2) *motor*, and (3) *associative*, according as they (1) receive a stimulation from a non-neural source, (2) transmit a stimulation to a muscle or gland, or (3) transmit between other neurons. A better terminology for the three classes

of neurons is (1) 'centripetal' or **afferent**, (2) 'centrifugal' or **efferent**, and (3) 'intermediate' or **central**. The peculiarity of the various parts of the brain and spinal cord, which are divided more or less completely into laterally symmetrical halves, makes it necessary to further divide the intermediate neurons of these structures into two classes: (a) those which run across from one half of brain or cord to the other half, (b) those lying entirely in one half, or in one half and peripheral structures. The (a) class are called **commissural** neurons, and the name *association* neurons refers strictly to the (b) class.

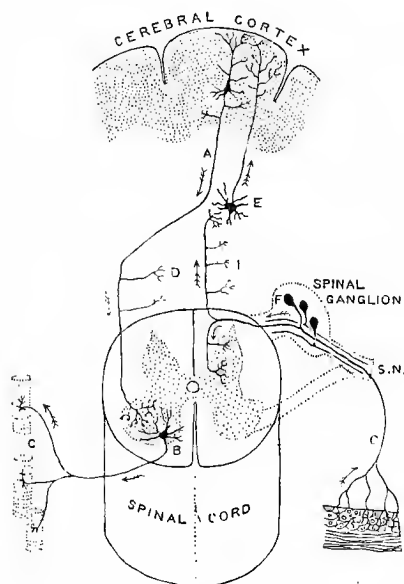


FIG. 33. Diagram of the simplest possible reflex arc from epidermis through cerebral cortex to striped muscle. (Cunningham, after Ramon y Cajal.) The arc, as drawn, involves four neurons. According to some, there is another synapse between *E* and the cortex, in the midbrain. There may be intermediate neurons in the cortex, forming links between the afferent neuron *E* and the efferent neuron *A*.

It is generally believed that the neurons are distinct individuals or structural units, and that where several neurons form a functional series or chain, the axon of one cell is merely in contact with the next cell, or with its dendrite. These points of contact between neurons; the points, that is, at which the stimulus is passed on from one to the other, are called **synapses** (singular either **synapse** or **synapsis**), or **synaptic points** [Figs. 32-34].

Both axons and dendrites may have many branches, like the rootlets of a tree. Thus, in certain parts of the nervous system, the terminations of one axon may be in contact with the dendrites or the cell-bodies of a number of other neurons, and conversely, the branches of a dendrite may be in contact with axon branches of several cells. Moreover, as many cells have many dendrites each, the multiplicity of possible connection from cell to cell is very important.

Although an axon cannot conduct a stimulus to a dendrite of the same

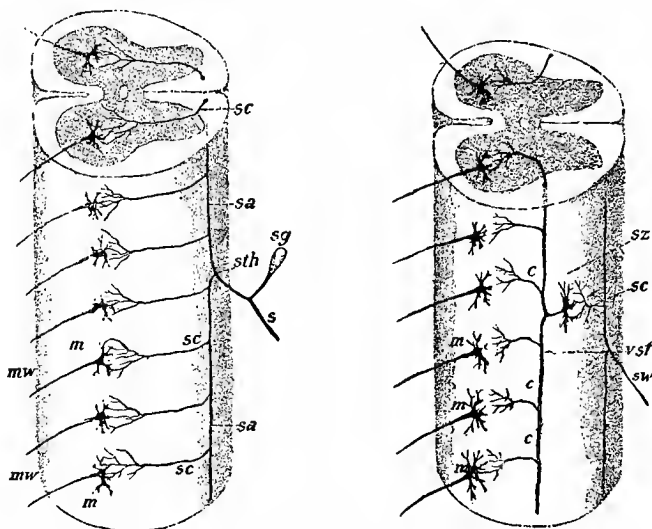


FIG. 34. Diagrams of reflex mechanisms in the spinal cord. (Barker, *Nervous System*, after Kölliker.) Left: two-neuron arc, *s*, *sg*, *sa*, *sc*, afferent neuron with ganglion cell (*sg*), and ascending and descending branches and collaterals within the cord. *m*, *n*, efferent neuron, with cell bodies in cord. Right: three-neuron arc. Only one collateral (*sc*), of the afferent neuron is shown. *c*, *c*, associative neuron.

cell, a stimulation may be received by one branch of an axon and transmitted to other branches of the same axon. Thus, if a single muscle fiber is caused to contract it may irritate the axon branch applied to it, and cause the contraction of another fiber supplied by another branch of the same axon.

THE STRUCTURE AND INVESTITURE OF NERVE FIBERS AND NERVES.

The fibers (axons or dendrites) consist of longitudinal **fibrils** embedded in a protoplasm which is called **neuroplasm**. These fibrils seem to run through the cell-bodies, and thus the fibrils in axon and dendrites

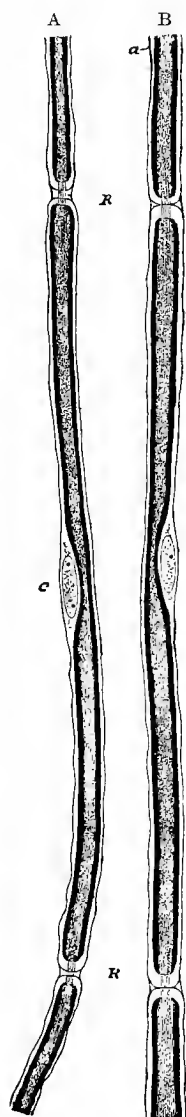


FIG. 35. Portions of two medullated axons from rabbit. Magnified 425 diameters. (Schäfer, *Microscopic Anatomy*.) *R, R*, nodes of Ranvier, dividing the medullary sheaths into segments. *a*, neurilemma. *c*, nucleus and cytoplasm of neurilemma. The myelin is stained black in this preparation.

would be continuous. This is not certainly established. All nerve fibers which pass beyond the immediate vicinity of their cell-body seem to be provided with one or more coverings. Three types of coverings have been distinguished. A. A coat of delicate cells whose origin is from the neural crest. This is the **neurilemma**, or **sheath of Schwann**. B. A connective tissue sheath: the **sheath of Henle**. C. A coating of **myelin**, a fat-like substance held in suspension in a network of another substance called *neurokeratin*. Some histologists have described a fourth type of sheath.

It is probable that all fibers have a neurilemma, except those in the 'gray matter' of the nerve centers. In all cases, however, the neurilemma is absent for a short distance after leaving the cell-body, and again at the farthest end. Most observers claim that fibers in the white matter of the brain and cord have no neurilemma: Ramón y Cajal, however, finds

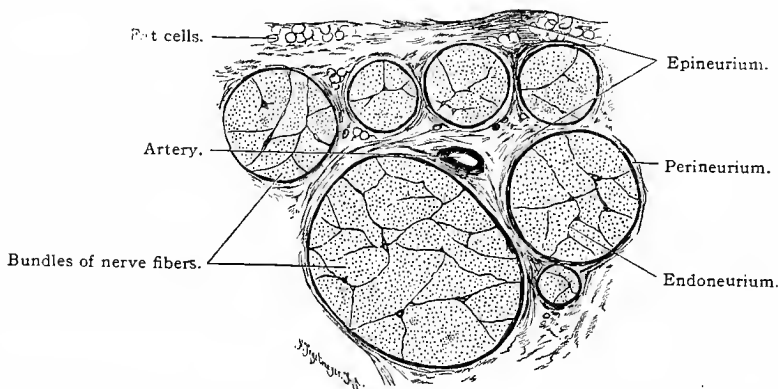


FIG. 36. Cross-section of a portion of a human nerve. Magnified about 20 diameters. (Lewis and Stöhr, *Histology*.) Seven funiculi are shown; these are composed of bundles of medullated nerve fibers with irregular septa of endoneurium and are wrapped in lamellar fibrous perineurium. The areolar epineurium which binds the funiculi together contains many fat cells.

the neurilemma on some of those fibers. All fibers in the 'white' matter of the brain and cord, and most fibers elsewhere, have the myelin (and neurokeratin) sheath for a portion of their course, at least, and are called **medullated** fibers. The fibers which have not the myelin sheath are called **non-medullated**, these latter belonging chiefly to the visceral system.

The myelin sheath, when it is present, always lies next to the axon, under the neurilemma (if the latter is present). The connective tissue sheath, which is found only in peripheral fibers, is outside the neurilemma.

Medullated nerve fibers have the myelin deposit interrupted annularly at intervals of from 80μ to a millimeter along it; the interruptions are known as the **nodes of Ranvier** [Fig. 35]; all branches of medullated fibers appear at these nodes. As there is but one nucleus for every internodal segment of the myelin sheath, such segments are thought by some histologists to be each developed from a single cell, the neurilemma corresponding to the cell-membrane, and the neurokeratin to the spongoplasm.

The nerve-fibers are, except at their terminations, associated in bundles called **nerves**. These are spoken of as *medullated* and *non-medullated*, according as they are made up of medullated or non-medullated fibers. The larger medullated nerves are made up of a number of bundles (called **funiculi** or **fasciculi**), each surrounded by a sheath of dense connective tissue (**perineurium**) which is continuous with the sheath of Henle surrounding each fiber, the whole nerve being surrounded by a layer of loose connective tissue, the **epineurium** [Fig. 36].

The **spinal cord** lies in the **cervical**, **thoracic** (or 'dorsal') and **lumbar** portions of the **spinal canal** of the vertebral or spinal column [Fig. 38]. The spinal column is composed of 33 **vertebrae** [Fig. 39] articulated together, each vertebra, except the lower, false or fixed vertebrae, having back of its 'body' a vertical opening, somewhat annular in cross-section, the **spinal foramen**. These foramina are segments of the spinal canal, the walls of which are, therefore, partly the foramen walls and partly the ligaments uniting the vertebrae.

The 'pedicles' of the cervical, thoracic, and lumbar vertebrae (exclusive of the upper ones, the 'atlas' and the 'axis') joining the 'body' of each to its posterior portion, are notched, more deeply so on the under side ('inferior notch'), so that as the vertebrae are articulated, the 'inferior notch' of one and the 'superior notch' of the one below it form a lateral opening, the **intervertebral foramen**, through which run the nerves connecting the spinal cord with the trunk and limbs (the **spinal nerves**, of which there are 31 pairs).

The spinal ganglia of all the spinal nerves, except four pairs, lie in the intervertebral foramina [Fig. 40]. Thus they are protected by the bony column. The ganglia of the sacral and the coccygeal nerves lie in the spinal canal itself, and the ganglia of the first and second cervical nerves lie on the 'arches' of the first and second vertebrae.

The spinal cord is composed mostly of 'white' matter surrounding a core of 'gray' matter, the latter having in cross-section roughly the shape of the letter H [Fig. 41]. Outside the 'white' matter are three protective membranes [Fig. 40]: (1) the **pia mater**, a fibrous connective

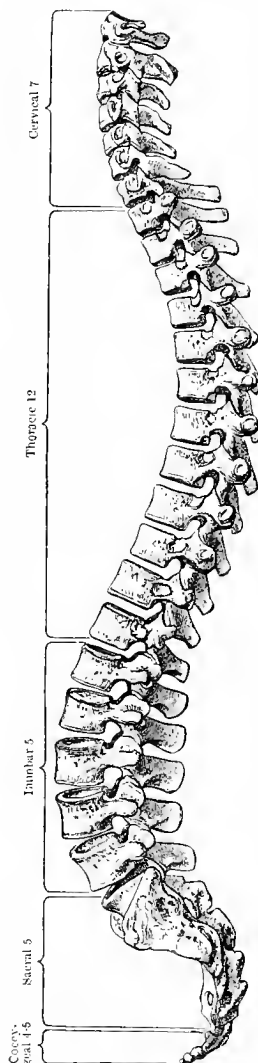
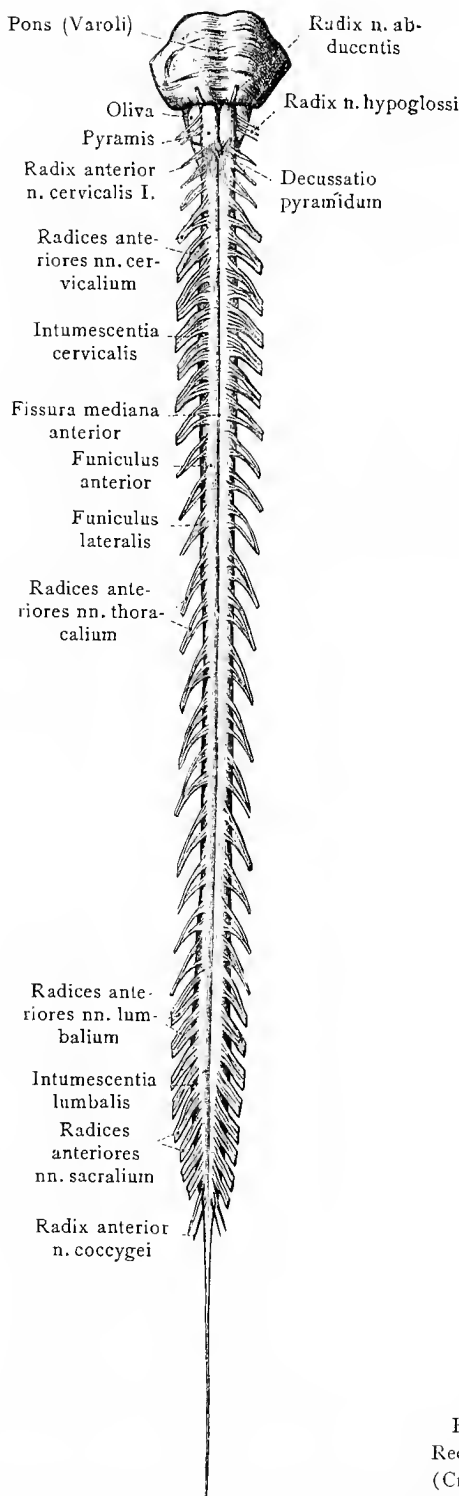


FIG. 38. Vertebral column, left view. Reduced to about one-third diameter. (Cunningham, *Anatomy*.)

FIG. 37. Spinal cord, anterior view. Reduced to about one-half diameter. (Toldt, *Anatomischer Atlas*.) Showing the roots (radices) of the spinal nerves, the lumbar and cervical enlargements (Intumescentiae), the pons, olives, and pyramids.

tissue coat, closely applied, continuous with the inner surface of which are fine *septa*, penetrating the 'white' matter; (2) the **arachnoid**, a thin membrane loosely wrapped around outside the pia mater, leaving an inter-

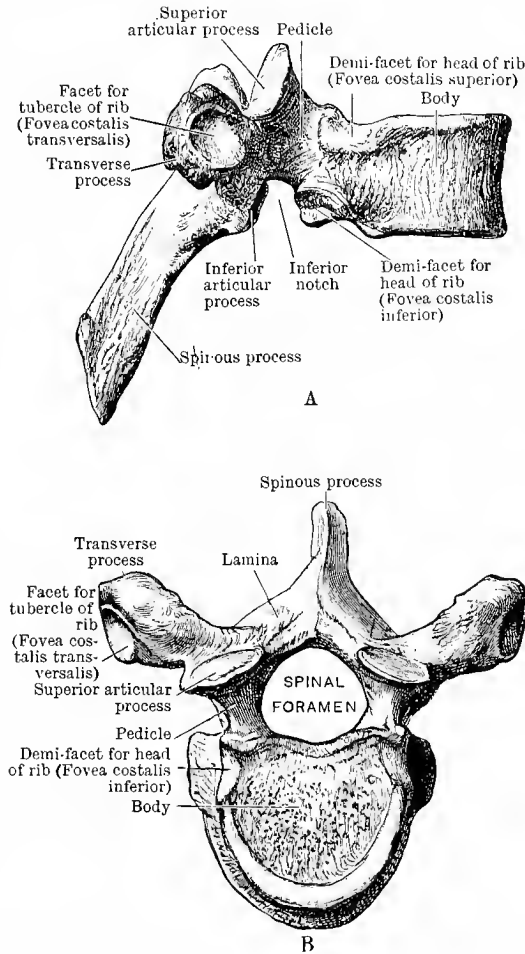


FIG. 39. Fifth thoracic vertebra, actual size. (Cunningham, *Anatomy*.) *A*, right view. *B*, from above.

val (the 'subarachnoid space') filled with 'cerebrospinal fluid'; and (3) the **dura mater**, forming a dense tubular sheath, considerably larger than the cord, and extending downwards below the limit of the cord into the

sacral part of the canal. The cord is attached to the inner surface of the sheath of dura mater by two lateral wing-like **ligamenta denticulata**.

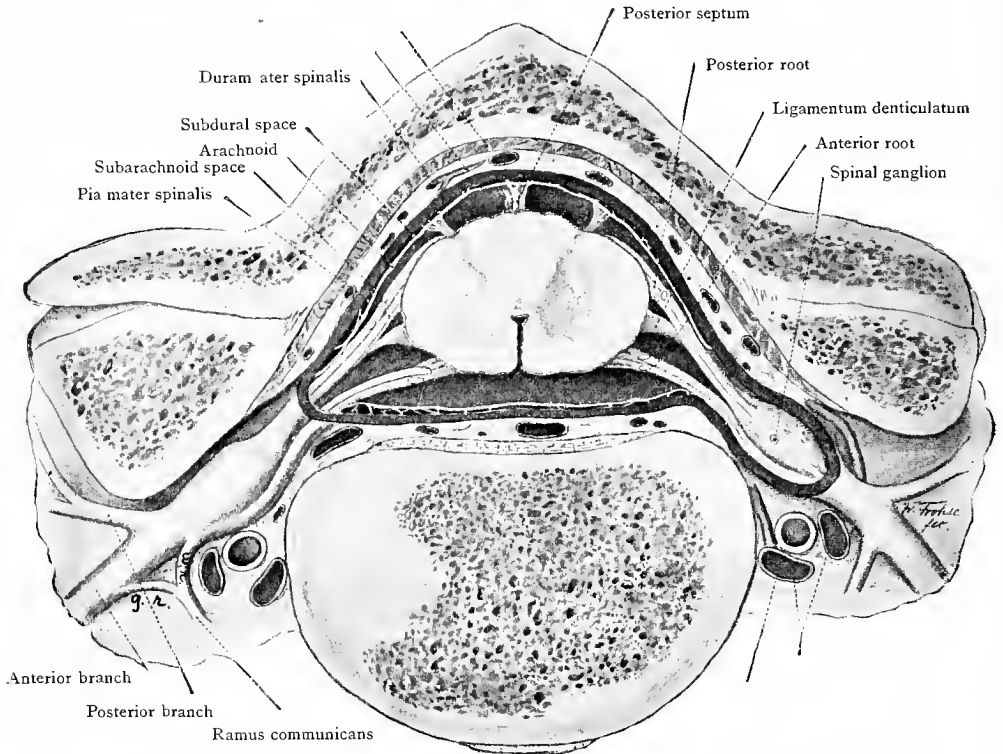


FIG. 40. Cross-section through fourth cervical vertebra, showing cord and its coverings. Enlarged about two diameters. (Bailey, *Histology*, after Rauber-Kopsch.)

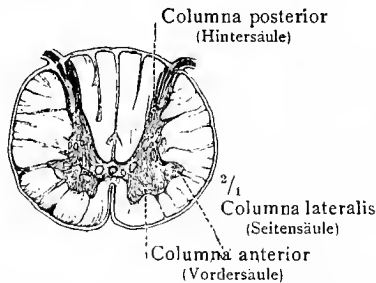


FIG. 41. Cross-section through spinal cord of adolescent, at level of first cervical nerve. Magnified two diameters. (Toldt, *Anatomischer Atlas*.)

Between the dura mater and the wall of the spinal canal is a small space filled by fatty tissues and blood vessels.

On the anterior and posterior sides of the cord there are *fissures*, into

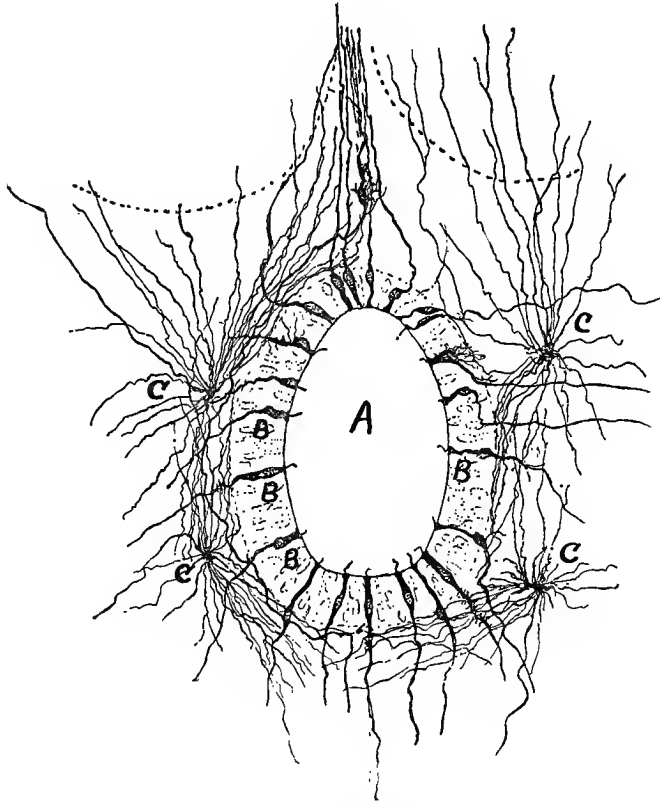


FIG. 42. Ependymal and neuroglia cells in embryonic spinal cord. Enlarged. (After v. Lenhossék.) *A*, central canal. *B, B*, ependymal cells; modified neuroglia cells composing the epithelium lining the canal; only a few are stained. *C, C*, typical neuroglia cells in the gray matter of the cord.

each of which a fold of the pia mater extends, nearly dividing the cord into two halves. A fold of the arachnoid (the *septum*) extends to the dorsal side of the cord, across and dividing the subarachnoid space,

GRAY MATTER AND WHITE MATTER.

The 'white matter' of the brain, cord and nerves is made up chiefly of medullated nerve fibers, running through the framework of **neuroglia**,

The 'gray matter' (found only in brain, cord and ganglia) is composed of cell-bodies, and non-medullated fibers, in a neuroglia framework.

Neuroglia is composed of branched or fibrillated cells (neuroglia cells; derived from the same embryonic layer as the nerve cells) whose branches anastomose, forming a reticular tissue or network [Fig. 42].

There appear to be two kinds of neuroglia cells, in the one of which the processes branch repeatedly, in the other of which (the 'spider cells') the processes are entirely unbranched.

THE 'CEREBRO-SPINAL' AND 'SYMPATHETIC' SYSTEMS.

It is customary to class together the neurons whose cell bodies lie in the brain, cord, spinal ganglia, ganglia of the cranial nerve roots, and 'sense organs', as the **cerebro-spinal system**. The neurons whose bodies lie in the other ganglia ('sympathetic' ganglia) are classed as the **sympathetic** or **autonomic system**. This classification is useful if it is understood that there are not two separate systems, but two intimately associated parts of one system. Classification and terminology in respect to these divisions of the total nervous system are not well agreed upon. We shall refer to this point later.

REFERENCES ON NERVE TISSUES.

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Howell, *Physiology*, Chapters III and V.

Starling, *Physiology*, Chapter VI, §§ I-VI.

Bailey, *Histology*, Chapter V.

Schäfer, *Microscopic Anatomy*, § Structure of the Tissues, Sub-§§ The Tissues of the Central Nervous System.

Cunningham, *Anatomy*, § The Nervous System, Sub-§§ The Cerebrospinal System, and The Spinal Cord.

Lewis and Stöhr, *Histology*, Part I, § II, Nervous Tissue.

Schäfer, The Nerve Cell. In Schäfer's *Physiology*.

CHAPTER V.

THE AFFERENT AND EFFERENT NEURONS.

THE cell-bodies of the afferent neurons (so-called 'sensory' neurons) are found in: (1) the spinal ganglia, the ganglia of the cranial nerve roots, and the sympathetic and collateral ganglia. Here are located the bodies of the neurons whose dendrites extend to the skin, subcutaneous tissues, muscles, bones and tendons and viscera of the body; (2) the retina of the eye, the cochlea of the ear, and the olfactory membrane of the nose.

THE AFFERENT NEURONS OF THE SPINAL GANGLIA.

The afferent neuron cells in the spinal ganglia are modifications of

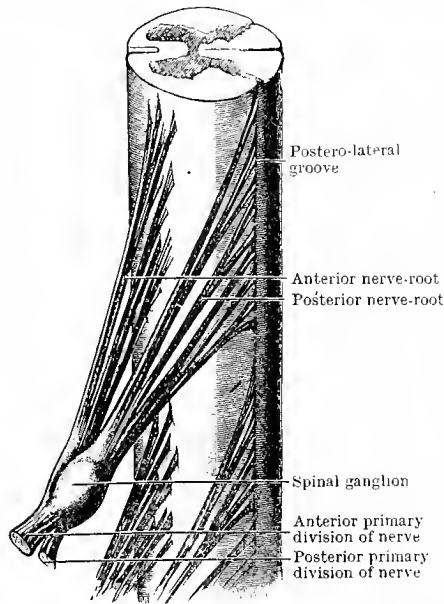


FIG. 43. Portion of cord, showing the roots and spinal ganglia of the seventh thoracic nerve. Enlarged about two diameters. (Cunningham, *Anatomy*.)

bipolar cells, *i. e.*, cells having one axon and one dendrite growing from approximately opposite sides; in the process of development the axon and

the dendrite move together, and fuse for a short distance of their length, giving rise to a T-shaped process [Fig. 44]; hence these cells are sometimes called **T-cells**, and (incorrectly) 'unipolar' cells. (There are true unipolar cells found elsewhere.)

The axon of the cell is sent into the spinal cord through the posterior root. Each posterior root, on entering the cord, divides into two bundles. The smaller bundle passes to the outer side of the tip of the posterior horn ('Lissauer's' tract) where each fiber bifurcates, one branch running up the cord and the other down. These branches run only a short dis-

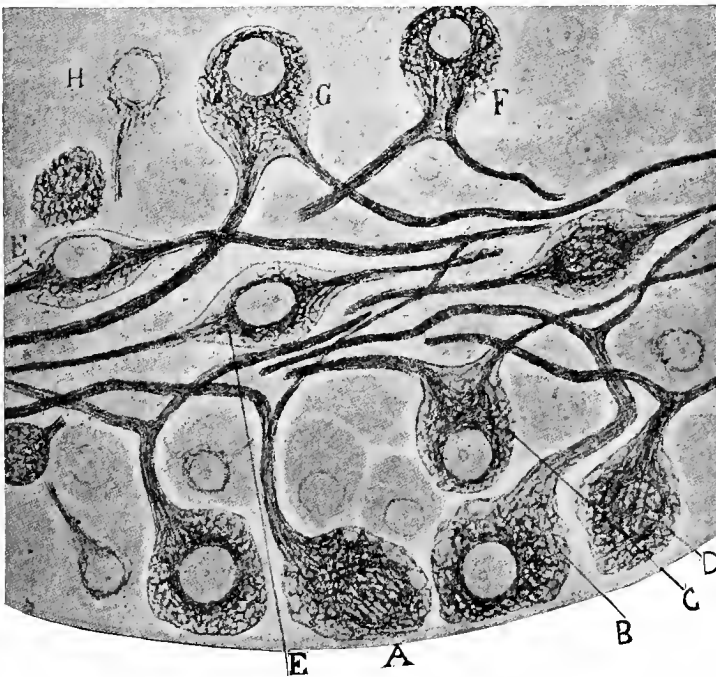


FIG. 44. Bipolar cells in a spinal ganglion of an embryo. Highly magnified. (Schäfer, *Microscopic Anatomy*, after Ramon y Cajal.) A, B, T-cells. E, E, cells still retaining the typical bi-polar form. C, D, F, G, cells in process of transition from the bi-polar to the T-form.

tance, sending off lateral branches which penetrate the gray matter and arborize around cells there.

The larger bundle of the posterior root fibers passes to the inner side of the horn and enters the posterior column, the fibers bifurcating, and one branch passes up and the other down as described for the fibers of the smaller bundle. The ascending branches of some of these fibers run up

to the medulla. The ascending branches of the other fibers run up a short distance and then into 'Clark's column' at the bases of the horns, arborizing there around cell-bodies whose axons run up to the cerebellum. Certain of the posterior root fibers arborize around cells in the anterior horn, *i. e.*, motor cells.

All these ascending and descending branches send lateral branches into the gray matter of the cord, as do the fibers of the other bundle.

The dendrites of some of the T-cells probably pass from the nerve over the white **ramus communicans** to the sympathetic and collateral ganglia; whether these fibers continue without interruption through the ganglia to the visceral tissues, or whether they are relayed, receiving stimulations from cells in the sympathetic or collateral ganglia, does not seem clearly made out. The other dendrites pass out over the spinal nerves to terminations in skin, subcutaneous tissues, muscle and tendon, and are properly called *somatic* afferent neurons.

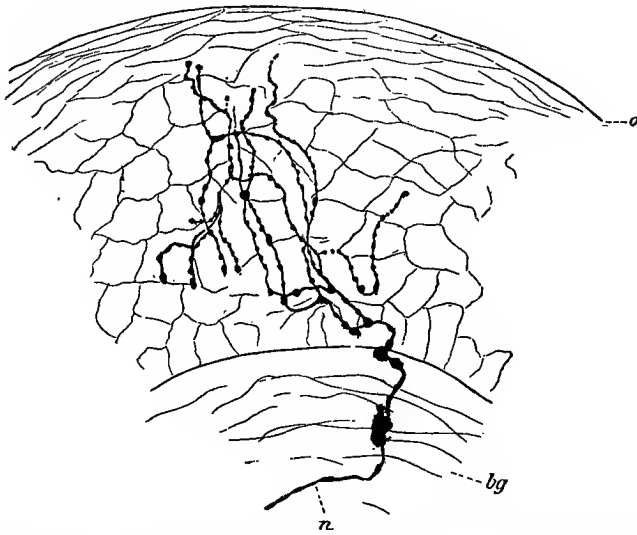


FIG. 45. Free nerve endings in the epithelial lining of the esophagus of a rabbit. Highly magnified. (Barker, *Nervous System*, after Retzius.)

AFFERENT NERVE ENDINGS.

The dendrons of afferent neurons end in four ways: 1. 'free'; 2. in contact with specially adapted epithelial cells; 3. in special structures or 'end organs' of connective tissue, 'encapsulated endings'; and 4. the dendrite in certain cases is modified, forming a characteristic end organ which is a part of the neuron itself.

FREE NERVE ENDINGS.

The fibers are said to end **free** when there are no specific 'end organs' in connection with them [Fig. 45]. Free endings are found chiefly in epithelial tissues (skin, mucous membrane, cornea of eye, etc.), although they may be present in other tissues.

When afferent fibers terminate in the 'free' way, they usually branch several times in sub-epithelial tissues, and lose first (as we approach the epithelium) the connective tissue sheath, then the medullary sheath, and finally the neurilemma. Then, nearer the epithelium, the branches of several fibers form a 'skein' or network of fibrils called *primary plexuses*. From these plexuses branches are given off which form *secondary plexuses*, still nearer the epithelium. Finally, fibrils proceed from the secondary plexus and ramify among the epithelial cells. The actual nerve endings, or endings of the ultimate branches, are 'free varicose fibrils'.

TACTILE DISCS.

In some cases (in deep layers of stratified epithelium) the fibrils terminate in flattened or saucer-shaped plates, **tactile discs** [Fig. 46], applied to epithelial cells (called *tactile cells*) as is the cup to an acorn.

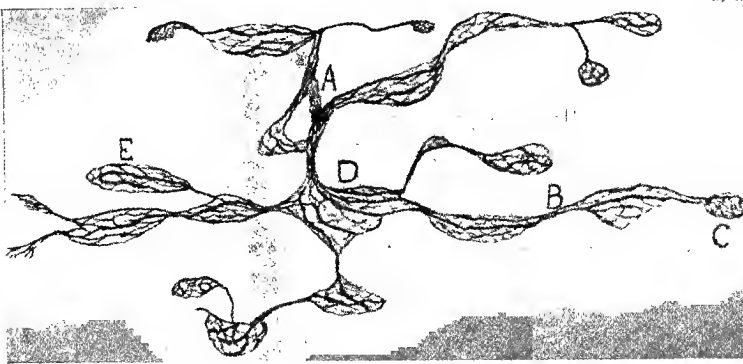


FIG. 46. Tactile discs. Highly magnified. (Ramon y Cajal.) These flat expansions of the fibers, containing net-works of fibrils, lie between the cells in epithelial tissues.

The tactile discs in the human being are especially numerous in the skin over the thighs and abdomen.

THE AUDITORY AND GUSTATORY ENDINGS.

The dendrites of the neurons located in the spinal ganglia of the cochlea pass out, through the spiral lamina, and their branches are applied to the

hair cells [Fig. 47]. These hair cells are columnar epithelial cells, from the free extremities of which bundles of cilia (auditory hairs) project. These cells are specialized receptors for auditory stimuli, and pass the stimulus on to the dendritic branches in contact with them. The auditory hair cells are arranged in a single or double row on the 'inner' side of the organ of Corti; and a triple or quadruple row on the 'outer' side. There are possibly from 20,000 to 25,000 of these hair cells in an ear in the

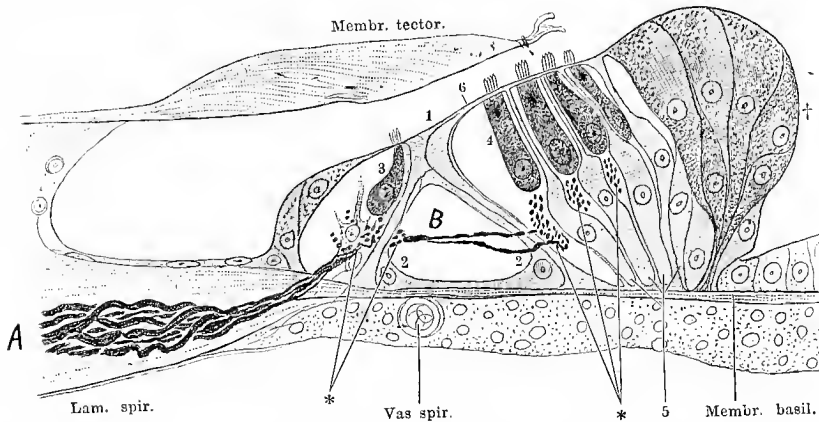


FIG. 47. Cross-section of the organ of Corti, showing nerve endings in the cochlea. Magnified probably 500 diameters. (Modified from Merkel-Henle, *Anatomie*.) The fibers (A) are seen emerging from the lamina spiralis, some terminating synaptically about the inner hair cells, (3), and the remainder crossing the 'tunnel of Corti' (B) to terminate around the outer hair cells (6). The black dots (*) represent cross-sections of the convolutions of the nerve fibers.

human being. In the vestibule and semicircular canals of the ear are small hair cells, not serially arranged, in contact with which are the branches of nerve fibrils from the vestibular branch of the cochlear nerve.

A somewhat similar form of end cell is in contact with the terminations of the gustatory nerve fibres in the tongue (fibers of the 9th or *glossopharyngeal* nerve and of the lingual branch of the 5th or *trigeminal* nerve). This is the **gustatory cell**, found in the **taste bud** [Fig. 49]. Taste buds are irregular ellipsoid or conical bodies 70-80 μ in diameter, lying in the epithelium of the mucous membrane, most numerous in the sides of the annular groove in the circumvallate papillae [Fig. 48] (probably 100 to 150 for a single papilla). They are found in smaller numbers in the 'foliate papillae', and on the edges and tip of the tongue. Sometimes buds are found in the 'fungiform papillae', the soft palate, the

posterior surface of the epiglottis, and occasionally in the lining of the cheek.

Taste buds are composed of two kinds of cells: **gustatory** and **supporting cells**. The supporting cells form the enclosing walls of the bud, and are also found inside it between the gustatory cells. These latter are in general elongated and spindle-shaped, although found in various wedge and other shapes. At the outer edge of the bud is a small opening; the **inner taste pore**, from which a **pore-canal** leads between the epithelial cells to the surface of the epithelium, terminating in the **outer taste pore**.

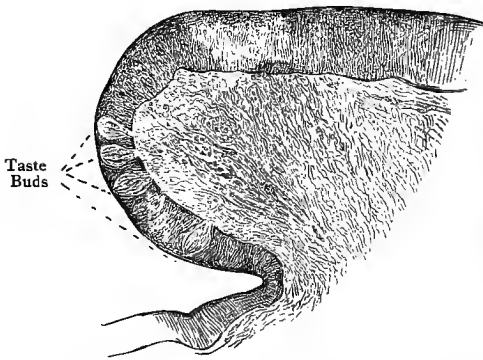


FIG. 48. Vertical cross-section of a *papilla circumvallata*, showing taste buds in the side. Magnified probably 100 diameters. (Merkel-Henle, *Anatomie*.)

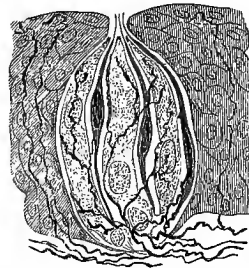


FIG. 49. Taste-bud, schematic. Magnified probably 500 diameters. (Merkel-Henle, *Anatomie*.)

The gustatory cells have stiff hair-like processes (**cilia**) extending through the inner pore into the pore canal. The number of gustatory cells in a bud varies; sometimes there are only two or three; sometimes they are as numerous as the supporting cells.

The fibers of the glosso-pharyngeal and lingual nerve form plexuses below the epithelium, and from these two sets of fibers rise, one set ending free, in numerous knobbed branches between the epithelial cells, and the other set entering the taste buds, at the bottom, usually from two to five for each bud. Inside the bud the fibers divide, multiply, and the branches end (usually with minute knobs) between the gustatory and supporting cells.

CORPUSCULAR AND SPINDLE ORGANS.

There are several forms of end organs which may be described as connective tissue **corpuscles** or **capsules**, containing a **core** of soft material

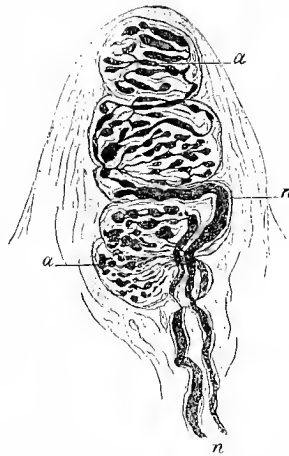


FIG. 50. Longitudinal section of tactile papilla, containing a Meissner's corpuscle. Magnified probably 400 diameters. (Ranvier, *Histologie*.)

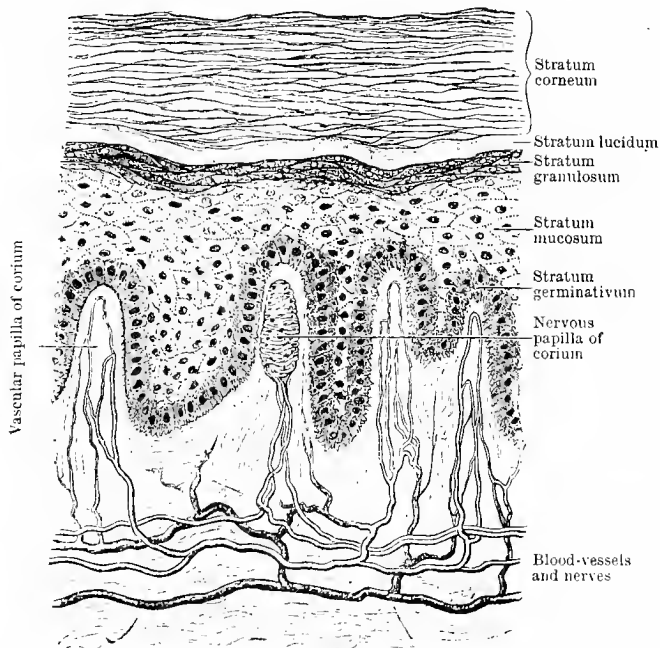


FIG. 51. Section through human skin, showing the layers of the epidermis and the papilla in the corium. Magnified probably 140 diameters. (Cunningham, *Anatomy*.)

which appears to be composed of nucleated protoplasm, within which the dendrite branches more or less complexly and terminates.

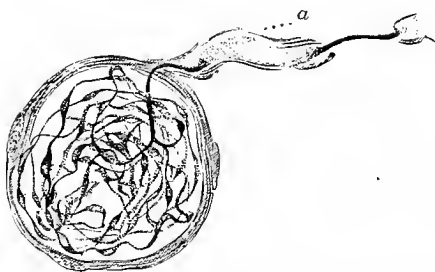


FIG. 52. Section through a terminal corpuscle (end-bulb of Krause), from the conjunctiva. Magnified probably 500 diameters. (Barker, *Nervous System*, after Dogiel.)

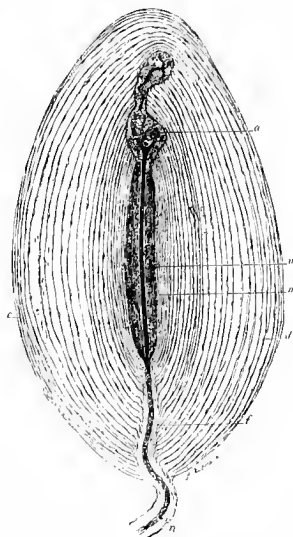


FIG. 53. Section of a Pacinian corpuscle. Magnified probably 50 diameters. (Ranvier, *Histologie*.) The nerve fiber, *n*, enters the capsule through the channel *f*, and has its terminal branches at *a*.

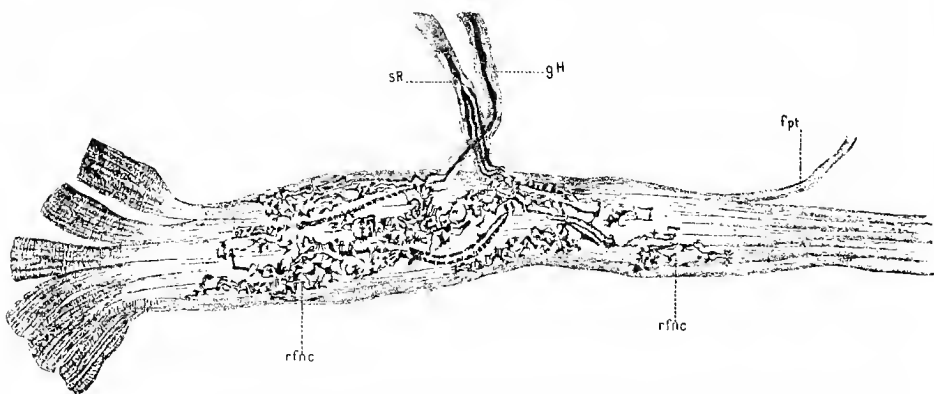


FIG. 54. A tendinous terminal organ ('organ of Golgi'), on the 'tendon of Achilles'. Magnified. (Barker, *Nervous System*, after Ciaccio.)

Tactile corpuscles (*Meissner's corpuscles*) and **end bulbs** (*end bulbs of Krause, genital corpuscles*, etc.) resemble enlargements of the fiber, cylindrical or spheroidal in the end bulbs, and ellipsoidal in the tactile corpuscles. The core contains several nucleated cells. The nerve fiber may wrap around the tactile corpuscle several times before entering it.

Tactile corpuscles [Fig. 50] occur in some of the papillae of the skin of the hand and foot, and more sparingly in the back of the hand, the inner surface of the forearm, the lips, eyelids, nipples, and external genital organs. End bulbs (other than the genital corpuscles) are often very small, but sometimes are over 50μ in diameter. Genital corpuscles are from 20μ to 350μ in diameter.

Tactile corpuscles are always within the connective tissue layer of the skin, the **corium** [Fig. 51]. They are from 80μ to 150μ in length, and $\frac{1}{3}$ as broad.

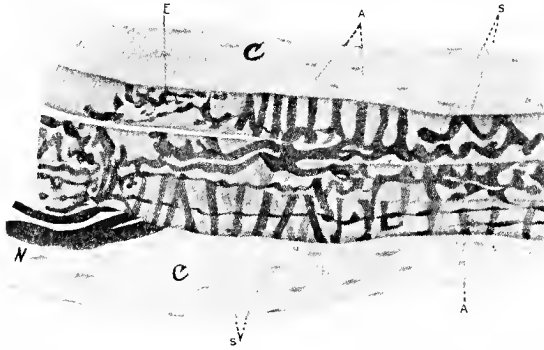


FIG. 55. Middle third of a 'terminal plaque' in a muscle spindle of a cat. Highly magnified. (Barker, *Nervous System*, after Ruffini.) At *N* are seen three nerve fibers, whose branches compose the rings (*A*), spirals (*S*), and branched processes (*F*) making up the 'plaque'. Three muscle fibers are shown, enclosed in the sheath *C*, *C*.

End bulbs [Fig. 52] are found in the conjunctiva in the corium in or below the papillae of the lips and tongue, in serous membranes, in tendons, aponeuroses, the epineurium of nerve trunks, in the neighborhood of the joints and in the corium of the modified skin covering the external genital organs.

Pacinian corpuscles (*Vater-Pacinian corpuscles; Golgi-Mazzonni corpuscles*) are larger than end bulbs, and formed with many concentric layers of connective tissue, like layers of an onion. A single medullated nerve fibre enters the corpuscle, losing its medullary sheath and branching within [Fig. 53].

Pacinian corpuscles are found in the subcutaneous tissues, in the corium, the hands and feet, in the periosteum of some bones,—in the neighborhood of tendons and ligaments, and in the connective tissues at the back of the abdomen. They are relatively large, being sometimes 1.5mm. in length.

TENDON AND MUSCLE SPINDLES.

A special form of ending, the **organ of Golgi**, is found in the tendons near the point of attachment of muscle fibers. The tendon bundle here becomes enlarged, and splits into a number (8 to 20) of smaller fasciculi.

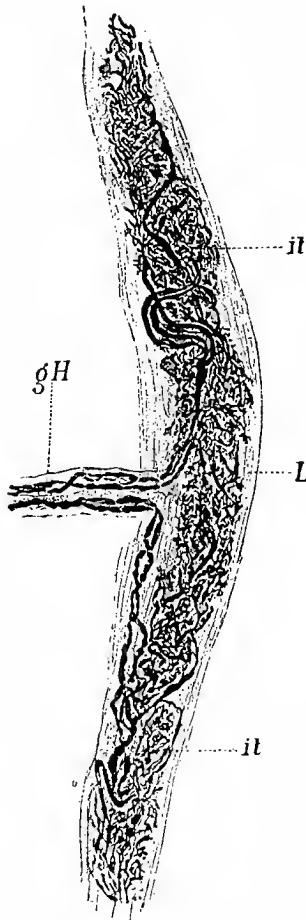


FIG. 56. A Ruffini's nerve ending. Highly magnified. (Barker, *Nervous System*, after Ruffini.) The ramifications of the nerve fiber *gH* are enclosed in the connective-tissue capsule *L*.

One or more nerve fibers penetrate between these fasciculi, losing their medullary sheaths, and arborizing there [Fig. 54]. The whole enlargement is enclosed in a connective tissue capsule continuous with the areolar tissue between the tendon bundles. Tendon spindles are from 1 to 1.5 mm. in length.

A somewhat similar mode of termination occurs in the **muscle spindle**. This consists of a connective tissue sheath enclosing a bundle of two to twenty or more muscle fibers (an 'intrafusal bundle') which are smaller

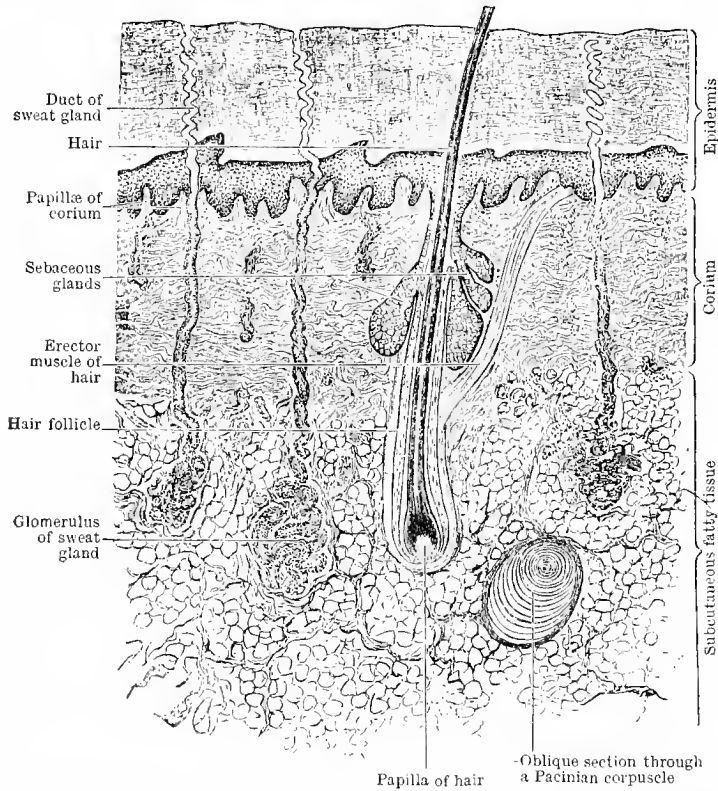


FIG. 57. Schematic vertical section through the skin, showing a hair, sweat glands, and sebaceous glands. (Cunningham, *Anatomy*.)

than the surrounding fibers and more like embryonic fibers. The subdivisions of some of the nerve fibers which enter the spindle wrap themselves spirally about the muscle fibers. The branches of others terminate in plate-like expansions applied to the fibers [Fig. 55].

Muscle spindles occur in the muscles generally, except in the tongue, where none have yet been discovered. Evans has found them to be especially numerous in the eye-muscles. They are from 1 to 5 or more mm. in length, and 1 to 3 mm. in the broadest parts.

RUFFINI'S ENDINGS

These are end organs lying at the junction of the corium and the subcutaneous connective tissue of the fingers and toes, and also deeper in the subcutaneous tissues. They resemble the spindle somewhat, having a connective tissue sheath within which the nerve fibers (in some cases two fibers) ramify [Fig. 56].

ENDINGS IN HAIR FOLLICLES.

In every hair follicle one or more afferent dendrites terminate. The hair follicle is a pocket in the skin, and hence consists of an outer sheath,

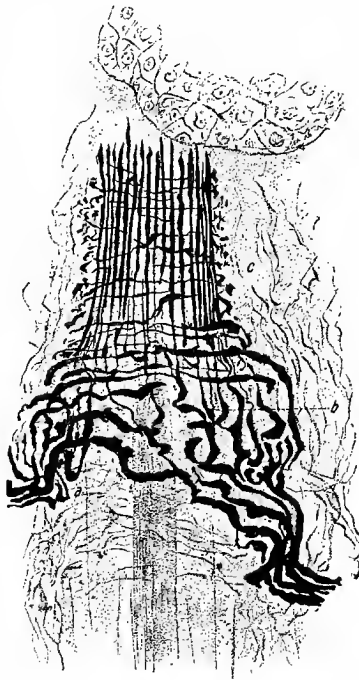


FIG. 58. Nerve endings about a large hair of a dog. (Barker, *Nervous System*, after Bonnet.)

the **theca**, continuous with the corium, and an **outer root sheath**, continuous with the deeper layers of the epidermis (*i. e.*, with the stratum

germinativum and stratum mucosum). Within them is an **inner root sheath**.

The theca is in three layers: an *outer* layer of loose tissue, a *middle* layer of compact circular bundles, and a thin *inner* layer, called the **glassy layer, (hyaline membrane or vitreous membrane)**.

The nerve fibre or fibres entering a follicle penetrate at about the median level to the glassy layer, where each forms two branches which almost completely encircle the hair, and on the opposite side arborize [Fig. 58]. The nerve terminals very rarely penetrate through the glassy layer.

Since hairs are present over the entire body except the palms of the hands, the soles of the feet, the dorsal surface of the terminal segments of the fingers and toes, and certain parts of the genital organs, it is apparent that they constitute an important group of receptor organs.

AFFERENT NEURONS OF THE OLFACTORY MEMBRANE.

The cell bodies of the olfactory afferent neurons are in the olfactory

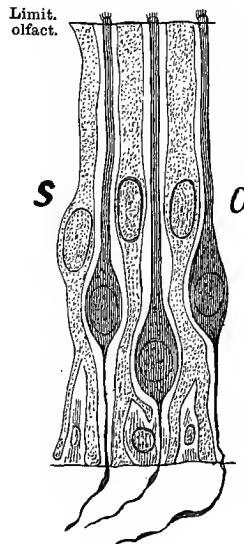


FIG. 59. Olfactory cells and sustentacular cells, schematic. Magnified about 800 diameters. (Merkel-Henle, *Anatomie*.) O, olfactory cell; s, sustentacular cell.

epithelium. Outwardly, the cell has a short slender process (corresponding to a dendrite) ending in a hemispherical knob that projects slightly beyond the general epithelial surface, and bears from six to eight stiff

The rod and cone may be considered as special forms of dendrites. The rod is connected with the cell body by a slender fiber, whereas the inner segment of the cone is practically a continuation of the cell body.

From the inner side of the cell body a short axon proceeds, which, in the case of the cone cell, has branches in contact with the dendrites of the **bipolar cells** in the 'inner nuclear layer' of the retina. The rod cell axons end in a single knob, in contact with the dendritic branches

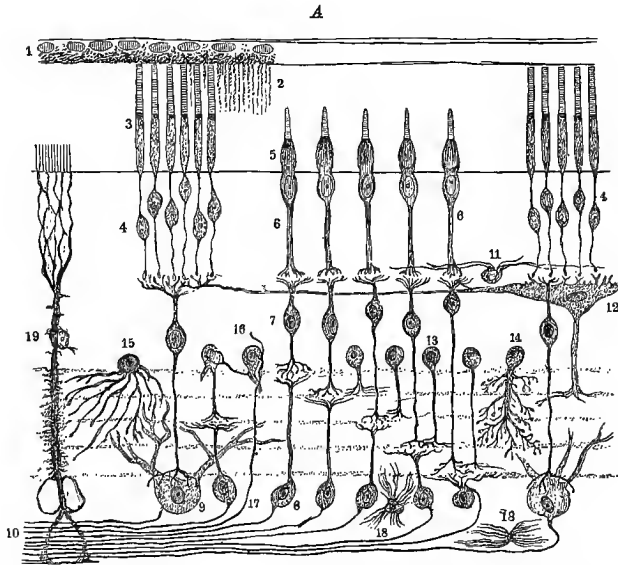


FIG. 61. Schematic representation of the sensory apparatus in the retina of the human eye. (Merkel-Henle, *Anatomie*.) 1, Layer of pigment cells next to the choroid. 2, Processes of the pigment cells. 3, Rods. 4, Bodies of rod-cells. 5, Cones. 6, Axons of cone cells. 7, Cone-bipolar cells. 8, 9, Ganglion cells. 10, Optic nerve fibers (axons of ganlion cells). 11, 12, Horizontal cells. 13, 14, 15, 16, Cells of different types; functions unknown. 17, Fibers (axons probably) of cells having bodies in the brain. 18, Neuroglia cells. 19, Radial fiber (Müller's fiber; part of the sustentacular syncytial framework of modified neuroglia).

of the bipolar cells. Each cone cell axon has synaptic connection with one cone-bipolar cell. The axons of several rod cells may arborize with the dendrites of a single rod-bipolar. In this layer there are also **horizontal cells** whose axon and dendrite branches are in contact with the terminations of the rod and cone cell dendrites. These horizontal cells are therefore interconnecting cells (so-called association cells).

The bipolar cells send axons inward to varying distances, which

touch the dendritic terminations of the **ganglion cells** in the next to the innermost layer of the retina, or possibly in some cases touch the ganglion cell bodies. These axons of these ganglion cells run to the **blind spot** or **disc** of the eye, and from thence in the optic nerve, to the **chiasm** (*chiasma opticum*), [Fig. 67], where the fibers for the right half of each retina pass to the right optic tract, and the fibers for the left half to the left optic tract. In each optic tract some of the axons run to the **external geniculate body** (*corpus geniculatum laterale*), [Fig. 69], and some to the **internal geniculate body** (*corp. gen. mediale*), on the same side, arborizing there in contact with interconnecting neurons, whose fibers continue in the optic tract to the 'occipital lobes' of the cerebral cortex, or run to other ganglia in the mid-brain.

THE EFFERENT NEURONS

The efferent neurons of the spinal system have their cell bodies in the gray matter of the cord, the axons leaving the cord on the anterior side (forming therefore the **anterior roots**), and joining the fibers of the



FIG. 62. End-plates (motor nerve endings) in striped muscle of a rat. Magnified 170 diameters. (Szymonowicz, *Histologie*.)

'posterior roots' to make the complete spinal nerve just beyond the 'spinal ganglion'. Some of these fibers (**somatic fibers**) run in the nerve and its branches directly to endings in striped muscles. Others, (**visceral** or **splanchnic** fibers) leave the nerve beyond the spinal ganglion

and run over the **white rami communicantes** to the ganglia of the sympathetic chain (the *lateral ganglia*). Certain of the splanchnic fibers arborize each around a number of cells in the sympathetic ganglia; others run through these ganglia to the **collateral ganglia**, arborizing in the same way there. The axons from lateral and collateral ganglia run to the smooth muscle tissue or to glands. Thus, the current leaving the spinal cord over a single splanchnic fiber is distributed finally to a number of axons. Many of the axons from the lateral ganglia return to the spinal nerve over the **gray rami** [Figs. 72, 73 and 74].

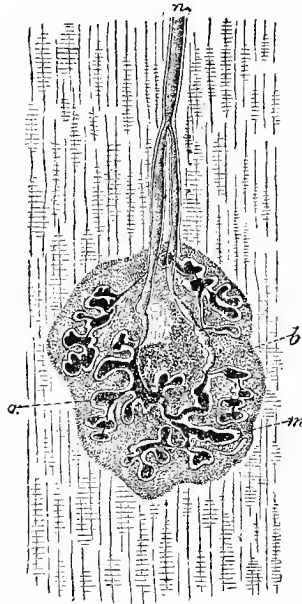


FIG. 63. End plate of a lizard. Enlarged 550 diameters. (Schäfer, *Microscopic Anatomy*, after Kühne.) *n*, Nerve fiber. *o*, Terminal ramifications. *m*, Matrix (clear substance surrounding the ramifications). *b*, Granular bed, or sole, of the end organ.

What has been said about spinal afferent neurons applies in general to the efferent neurons of the cranial nerves, whose cells lie in the nuclei of the medulla, pons and mid-brain.

As the fiber approaches its termination in voluntary (striated) muscle, it branches repeatedly, each fiber thus coming into relation to a number of muscle fibers. When a branch reaches a muscle fiber, the medullary sheath ceases abruptly, the neurilemma becomes continuous with the

sarcolemma beneath which the fiber branch terminates in the **end plate**, oval, from 40 to 60 μ in its longest diameter. Occasionally a branch terminates in two end plates. In this end plate, of nucleated protoplasm, the fiber arborizes, with enlarged ends [Figs. 62 and 63].

In smooth and cardiac muscle, the fibers of the terminal ganglia branch and pass between the fibrils, ending in enlarged outlets and knobs, in a fashion much simpler than that in the case of the striated muscle [Fig. 64].

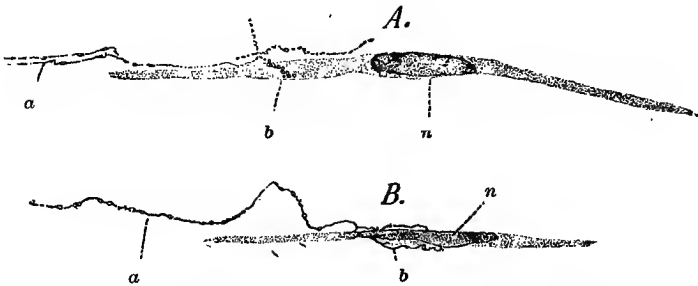


FIG. 64. Efferent nerve endings on smooth muscle fibers. Magnified probably 300 diameters. (Barker, *Nervous System*, after Huher and De Witt.)

Efferent nerve endings in glands are somewhat similar to the endings in smooth muscle, the branches of the fiber penetrating between gland cells and having spheroidal varicosities on their terminal segments. In some cases the final branches seem to enter the cytoplasm of the gland cells.

REFERENCES ON AFFERENT AND EFFERENT NEURONS.

- Lewis and Stöhr, *Histology*, Pt. I, § II, The Central Nervous System.
 Sherrington, *The Spinal Cord*. In Schäfer's *Physiology*.
 Schäfer, *Microscopic Anatomy*, § The Structure of the Tissues, Sub-§ The Tissues of the Nervous System.
 Barker, *The Nervous System*, Chapters XXVI-XXXVIII, LV-LVI.
 Bailey, *Histology*, Chapter XII.

CHAPTER VI.

THE GROSS RELATIONS OF NERVES, SPINAL CORD, BRAIN AND OTHER GANGLIA.

IN speaking of the human brain stem, the term 'anterior' means *upper* and 'posterior' means *lower*. These terms are used in this way because of the usual reference of the brain structures to the medullary tube from which the cerebro-spinal system develops. The brain develops from the anterior portion of this tube; the upper part of the brain stem (the fore-brain) develops from the most anterior portion. Moreover, in the quadrupeds, in which the cerebro-spinal axis is horizontal, the 'anterior' portions are really anterior to the 'posterior'.

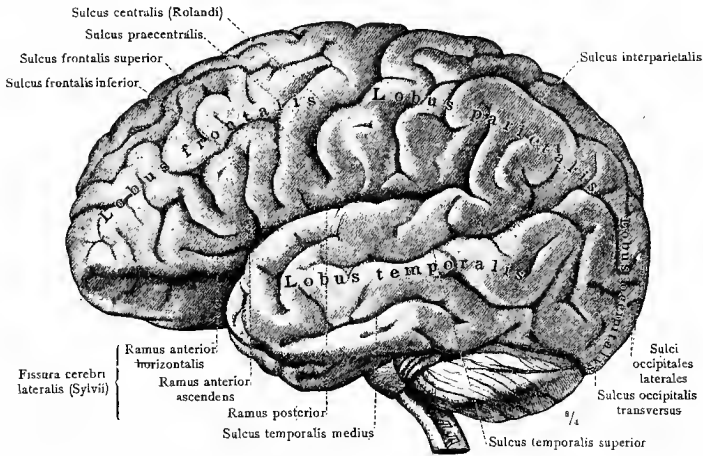


FIG. 65. Brain viewed from the left side, showing lateral surface of the left cerebral hemisphere. (Toldt, *Anatomischer Atlas*.) One-half normal size.

The **spinal cord** [Figs. 29, 37] extends from about the 'small' of the back into the skull, where it ends, at about the level of the ears, in the enlargement called the **medulla oblongata** (or *myelencephalon*), [Figs. 65-70], which is about an inch in length. Above the medulla on the front is a fibrous band, the **pons**, running horizontally across and into the **cerebellum**, which lies above and behind the medulla. (Pons and cerebellum together constitute the *metencephalon*). These are the three divisions of the **hind-brain** (or *rhombencephalon*).

Above the medulla and continuous with it is the **mid-brain** (or *mesencephalon*), about three quarters of an inch in length, on the back of which are the protuberances known as the **corpora quadrigemina**, and on the front the beginning of division into right and left portions, the **crura** (singular **crus**). This division becomes complete in the *diencephalon*, forming the two **thalami**, upon which are superposed the **corpora striata** [Fig. 70]. From the upper part of the thalami grow the **cerebral hemispheres** or **cerebri** (or *telencephalon*), which are the largest and most

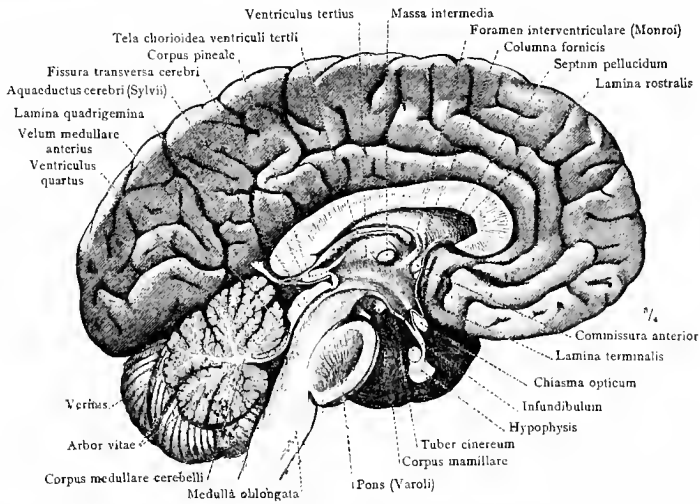


FIG. 66. Medial sagittal cross-section of brain, showing medial surface of left hemisphere, one-half normal size. (Toldt, *Anatomischer Atlas*.)

conspicuous parts of the brain, folding over and concealing nearly all of the mid-brain. Diencephalon and telencephalon together constitute the fore-brain (or prosencephalon) [Fig. 28].

The pons, medulla, mid-brain and thalami together make up the **brain-stem**.

It is important to distinguish certain parts and cavities of the brain, even if we make but a simple study of its structure, nervous connections and probable functions.

In all of these parts we find nerve cells, and also their axons and dendrites. The cell bodies are in general collected in the **cortex** or external portions of the cerebellum and cerebrum, and in groups scattered through the brain stem. These groups are called **nuclei**, and most of these nuclei have received distinctive names.

In addition to the substances of the brain, it is important to distinguish the cavities or **ventricles**, since it is often convenient to refer to the position of a nucleus or other detail as being in the **wall** of a certain ventricle, although the cavity may be relatively very small as compared with

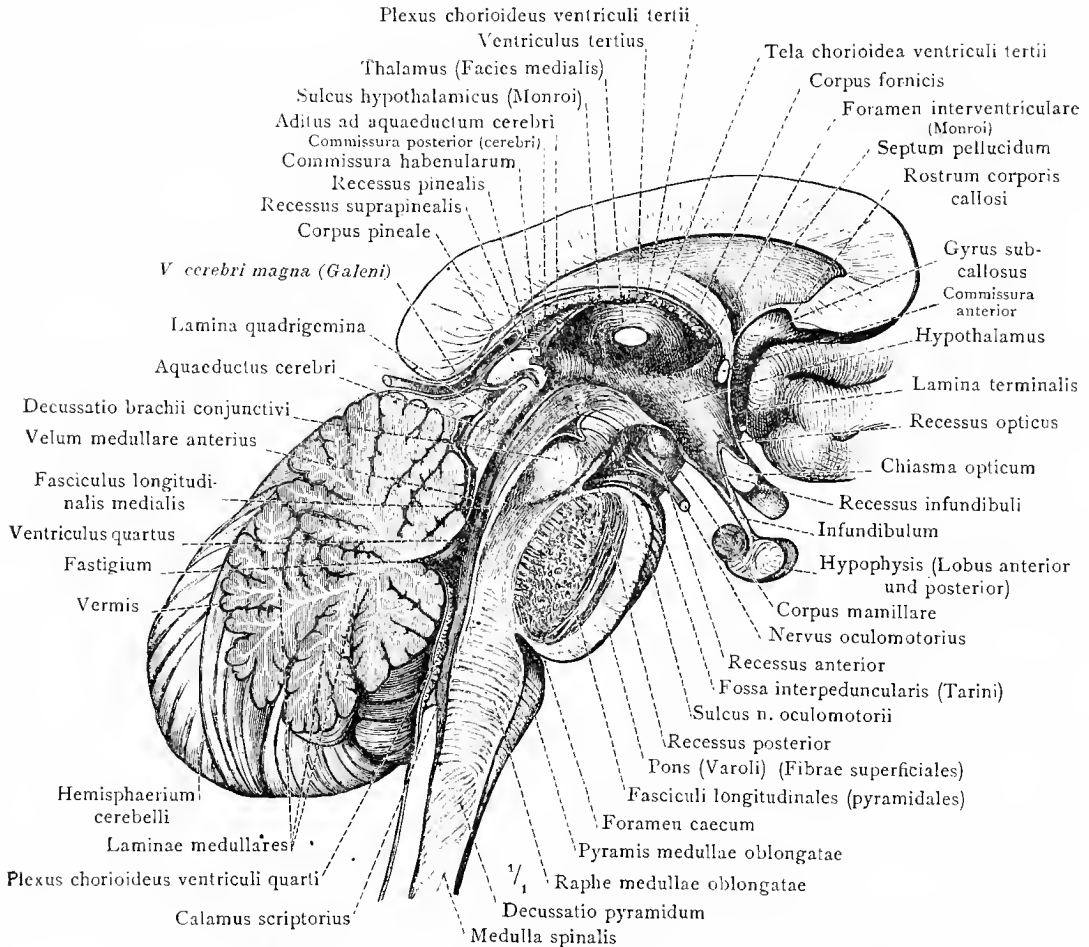


FIG. 67. Medial section of brain stem and cerebellum. (Toldt, *Anatomischer Atlas*.)

the thickness of the so-called 'walls'. In another respect the cavities are important, since the brain and cord are formed from a single tube, which, in the foetus, has a relatively large bore and thin walls, the brain and cord proper forming by actual thickening of these walls.

The cavities of the brain are as follows:

First and second ventricles (*ventriculi laterales*): hollows within the right and left cerebral hemispheres respectively [Fig. 70]. **Third ventricle** (*ventriculus tertius*), lying between the optic thalami, the inner surfaces of which form its side walls [Fig. 66]. The 'floor' or ventral boundary is formed by the *tuber cinereum*, the *corpora mamillaria*, the gray matter of the *locus perforatus posticus*, and the *tegmenta* of the

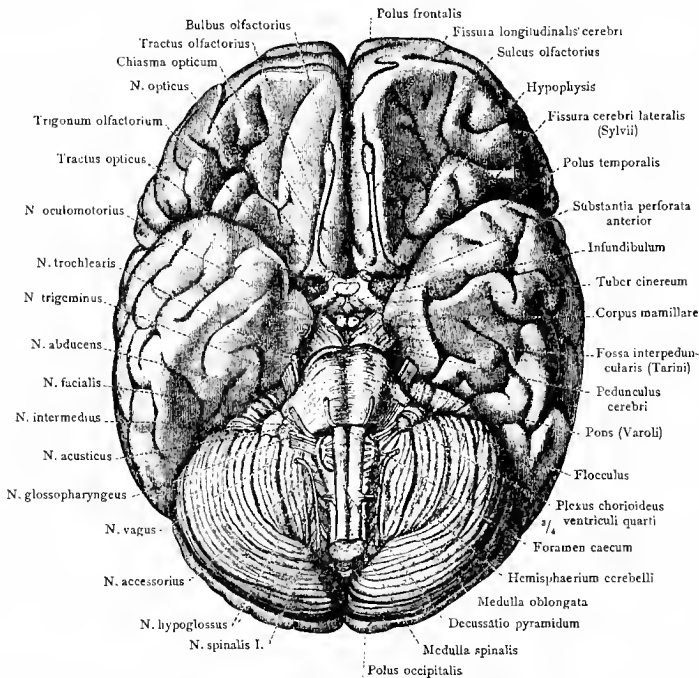


FIG. 68. Brain viewed from the front and below, one-half natural size. (Toldt, *Anatomischer Atlas*.)

crura cerebri. The 'frontal wall' or upper boundary is the *lamina cinerea*, and the 'roof' or dorsal boundary, an epithelial layer continuous with the epithelium lining the chamber. At the 'anterior' (or upper) end the third ventricle communicates with the first and second ventricles, and at the 'posterior' end it communicates through the **aqueduct of Sylvius** (*aqueductus cerebri*), a very small tubular aperture through the mid-brain, with the **fourth ventricle** (*ventriculus quartus*).

The fourth ventricle is the cavity under the cerebellum (the hind-brain), its ventral wall being the medulla, and its dorsal wall, a thin epithelial membrane.

The aqueduct of Sylvius and the third and fourth ventricles (except for the dorsal walls or 'roofs' of these latter) are surrounded by layers of gray matter, forming the nuclei of the third, fourth, sixth, twelfth and the cranial nerves, and the secondary nuclei of the eighth nerve, and of the afferent portions of the ninth, tenth and eleventh nerves. The nuclei for the fifth nerve and the efferent portions of the ninth, tenth and eleventh lie in the immediate neighborhood.

GROSS DETAILS OF THE BRAIN.

Certain details of the external appearance of the medulla, mid-brain and fore-brain are of importance both as indicating structural details and as points of topographical reference.

On the ventral side of the medulla the **olives** (*olivae*), the **pyramids** (*pyramis*), and the **decussation of the pyramids** (*decussatio pyramidum*), are noticeable [Fig. 68]. On the dorsal side the **cuneate tubercles**, the **clava**, the **funiculus gracilis**, and the **funiculus cuneatus** appear [Fig. 69A]. Above the medulla the **pons** appears on the ventral side, and the **cerebellum** on the dorsal, with **middle** and **superior cerebellar peduncles** (*brachia pontis* and *brachia conjunctiva*) joining it to the ends of the pons and to the brain stem behind the pons [Figs. 68 and 69].

Conspicuous on the floor and side walls of the fourth ventricle (between the stem and the cerebellum) are the **striae acusticae** (or *stria medullares*) crossing the **area acustica**, the **eminentia teres** (*colliculus facialis*) and the beginning of the **Sylvian aqueduct** (*Aqueductus cerebri*) [Fig. 69A].

The chief features of the mid-brain are the corpora quadrigemina on the dorsal surface (two pair, 'inferior' and 'superior' [Fig. 69A] and the **pineal body** (*corpus pineale*) above them [Fig. 66]. The ventral aspect shows the **crura** (singular *crus*) **cerebri** (*pedunculi cerebri*) with the **sulcus oculomotorius** separating them, and lying in front of the upper part of these, the **corpora mamillaria** [Fig. 67].

Still farther forward is the protuberance known as the **tuber cinereum** from which the **infundibulum** extends down to the **pituitary body** (*hypophysis*) [Fig. 66].

The mid-brain between the crura and the corpora quadrigemina is called the **tegmentum**. The ventral portions of the crura are called **crustae**.

The crustae of the crura are separate in the mid-brain. Above, the tegmentum also divides, and each half of the brain stem enters a **thalamus**. The thalami are ovoid masses of gray matter, divided into three nuclei, the *nucleus anterior* (or dorsal nucleus), the *nucleus medialis* and the *nucleus lateralis*.

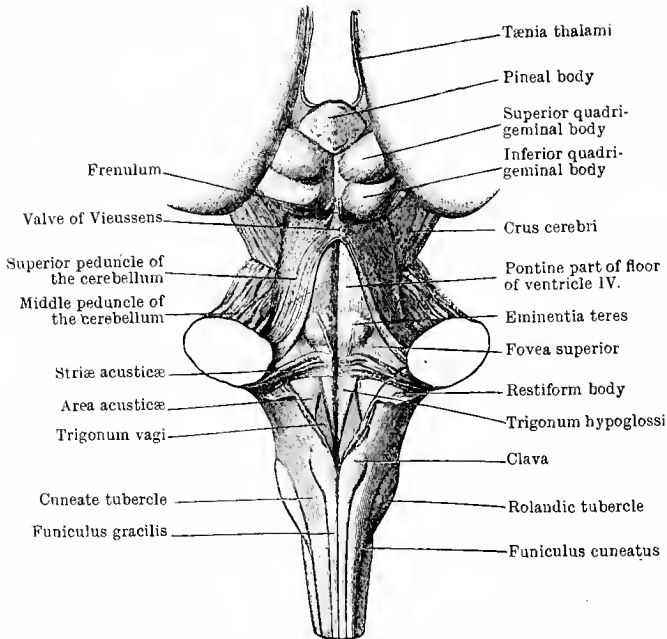


FIG. 69A. Floor of fourth ventricle, and rear of medulla and mesencephalon of full-time foetus. (Cunningham, *Anatomy*.)

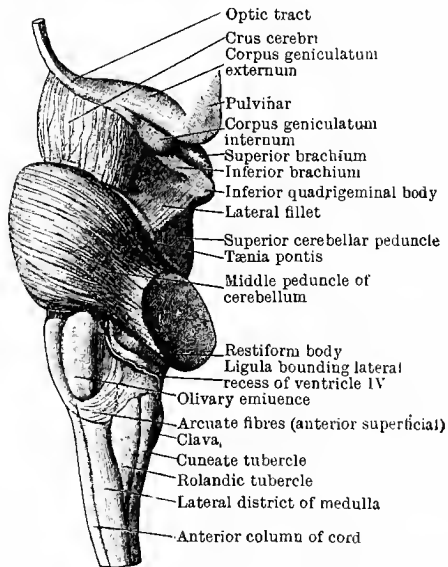


FIG. 69B. Brain stem of full-time foetus viewed from the left. (Cunningham, *Anatomy*.)

Laterally to each thalamus are two nuclei (*nucleus caudatus* and *nucleus lenticularis*), which together form the **corpus striatum**. Between these two nuclei a fan-shaped mass of nerve fibers (the **internal capsule**) runs up from the crusta. Lying behind the corpus striatus is another sheet of fibers; the **external capsule** [Fig. 70].

The dorsal projection of the thalamus is the **pulvinar**. Lying below and outwardly to the pulvinar are the **geniculate** bodies (two on each side), the external or lateral and the **internal or medial** [Fig. 69].

Above the thalami are the two **hemispheres** of the cerebrum which are spread out over and behind the thalami and the mid-brain. The hemispheres may be considered as ganglia, or groups of ganglia, the cells of which are in the outwardly lying portions (the **cortex**).

Running between the hemispheres is a broad band of fibers, the **corpus callosum**, and two other smaller bundles, the **anterior** and **posterior commissures**. (Many bundles of association fibers connect the various lobes of the same hemispheres).

Growing forward from the under side of each hemisphere near the brain stem is a long process, the **olfactory tract** (*tractus olfactorius*) at the end of which is the enlargement called the **olfactory bulb** [Fig. 68].

THE COLUMNS AND TRACTS OF THE SPINAL CORD.

In the 'white matter' of the cord three pair of **columns** are distinguished for convenience of reference [Fig. 41].

1. The **posterior columns**, lying between the 'posterior horns' of the gray matter, and separated by the **posterior fissure** of the cord.
2. The **lateral columns**, included between the anterior and posterior horn on each side.
3. The **anterior columns**, included between the anterior horns, and separated by the **anterior fissure**.

In the columns of the cord several distinct groups of fibers are distinguishable. The most important of these are as follows: the enumeration beginning at the dorsal fissure [Fig. 71].

I. **Ascending** (*i. e.*, conducting towards the brain). (a) The greater part of the posterior columns; specifically, the **column of Burdach** (*postero-lateral tract* or *fasciculus cuneatus*), and the **column of Goli** (*postero-mesial tract* or *fasciculus gracilis*). (b) **Lissauer's tract**, lying at about the apex of the posterior horn. (c) The **direct cerebellar tract** (*dorsal cerebellar tract*; *fasciculus cerebello-spinalis*; *Flechsig's tract*), and the **antero-lateral ascending tract** (*fasciculus antero-lateralis superficialis*; *Gower's tract*), occupying the superficial portion of the lateral column.

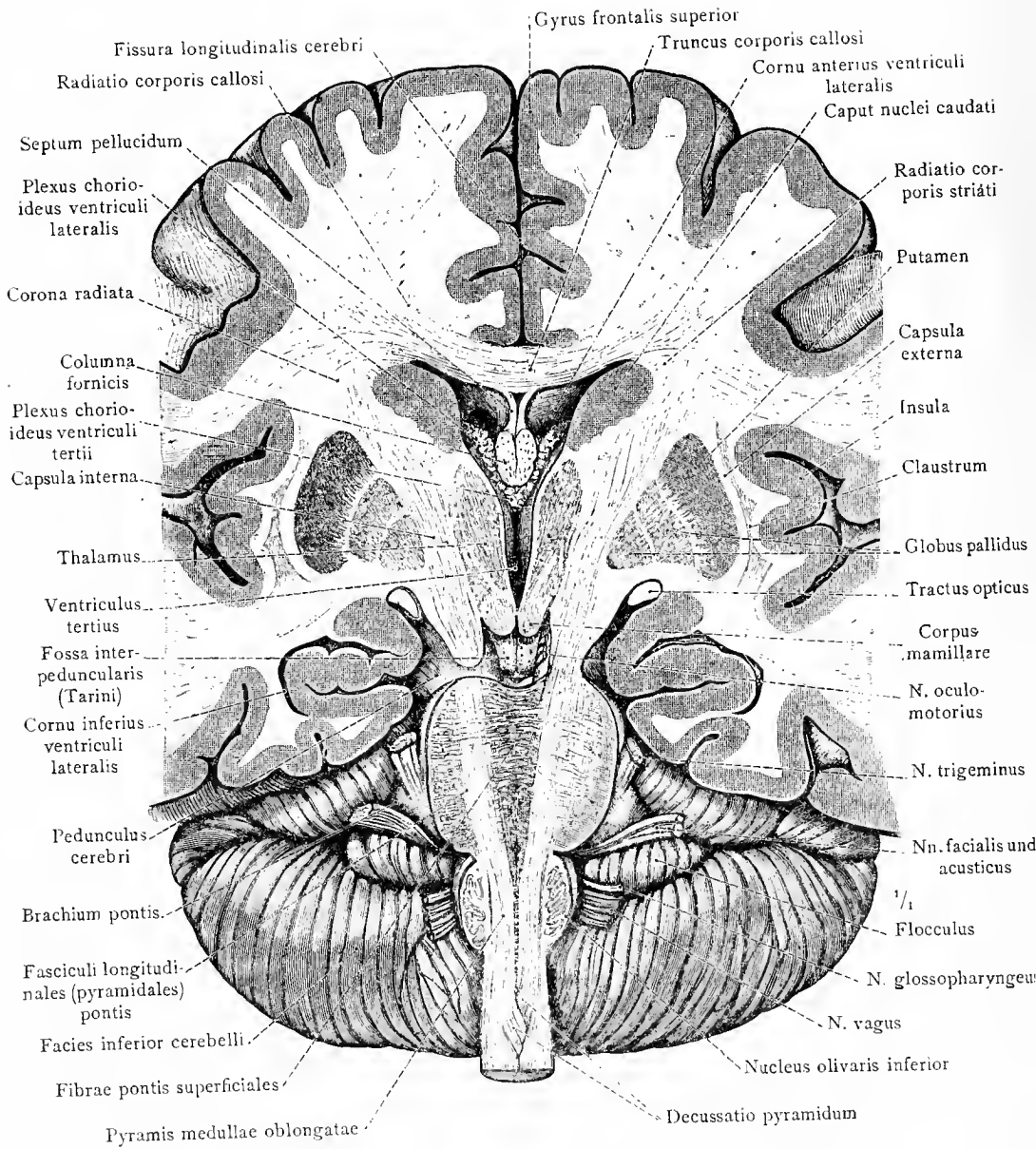


FIG. 70. Coronal section of brain. Normal size. (Toldt, *Anatomischer Atlas*.)

The fibers in the column of Goll and Burdach and Lissauer's tract are axons of the posterior roots, *i. e.*, whose cell-bodies are in the spinal ganglia. The fibers in the direct cerebellar tract have their cell-bodies in **Clark's Column**; a column of cells in the posterior horn. The location of the cell-bodies of the fibers in Gower's tract have not been definitely identified.

II. **Descending.** (a) The **septo-marginal tract**, lying in the edge of the posterior column close to the dorsal fissure. (b) The **comma tract**, lying within Burdach's column, close to Goll's. (c) The **crossed**

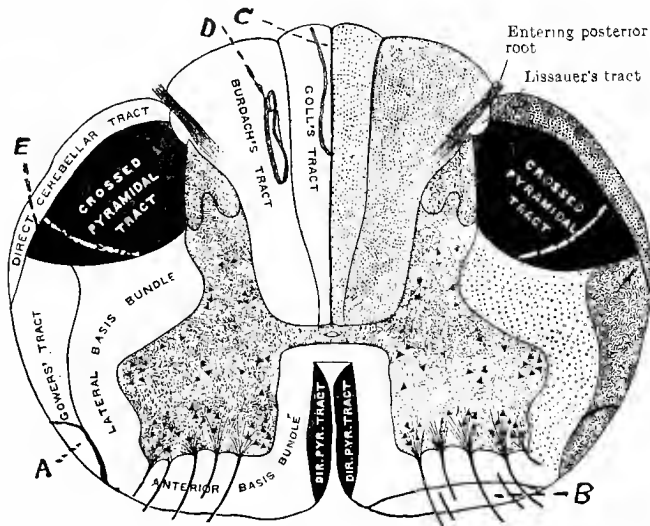


FIG. 71. Diagram representing a transverse section through the spinal cord. (Modified from Cunningham.) *A*, bundle of Helweg. *B*, descending antero-lateral tract. *C*, septo-marginal tract. *D*, comma. *E*, pre-pyramidal tract.

pyramidal tract (*fasciculus cerebro-spinalis lateralis*), and the **pre-pyramidal tract** (*rubro-spinal tract*; *von Monakow's tract*) lying in the lateral column. (d) The **spino-olivary column** (*bundle of Helwig*) lying superficially opposite the anterior horn. (e) The **antero-lateral descending tract** (*vestibulo-spinal tract*; *marginal bundle of Lowenthal*), marginally in front of the antero-lateral ascending tract. (f) The **direct pyramidal tract** (*fasciculus cerebro-spinalis anterior*), along the border of the anterior fissure. The fibers in the pyramidal tract are axons of cell-bodies in the cerebral cortex. The cell-bodies of the fibers in the other descending columns lie in the medulla, pons, cerebellum, or mid-brain, or gray columns of the cord.

III. Spinal interconnecting. The **basic bundles, anterior and lateral** (*fasciculus anterior proprius* and *fasciculus lateralis proprius*), are strands of fibers of cells in the gray matter of the cord, serving to connect the different segments of the cord with one another.

THE SPINAL AND CRANIAL NERVES.

The spinal nerves issue from the cord in pairs, a pair for each articulation of the spinal column. The nerve on each side has two **roots**, that is, it is made up out of two sets of fibers, one set efferent, issuing from the anterior horn of the gray matter of the cord, and the other (afferent) entering the cord on the posterior side. The spinal ganglion lies on the posterior root and the two roots are united in the intraspinal foramen just beyond the ganglion, forming a single nerve.

There are 31 pairs of spinal nerves, which are named, according to the position of their origins in the spinal cord, **cervical** (8), **thoracic** (12), **lumbar** (5), **sacral** (5), and **coccygeal** (1). These nerves are numbered in each group downwardly; thus, the uppermost spinal nerve is the '1st cervical', the next, the '2nd cervical', the ninth, the '1st thoracic', and so on.

The nerves issuing above the 1st cervical are called **cranial nerves**, and are numbered from one to twelve. When a nerve is referred to by number with no region assigned, 'cranial' is always meant. Only four of the cranial nerves are, like the spinal, 'mixed nerves'. Of the other eight, three are pure afferent, or 'sensory', and five are efferent, or 'motor'.

The cranial nerves, in order, as they are conventionally numbered, are given in the following list:

I. The **olfactory nerve** (afferent). This is not a 'nerve' in the usual sense, but a number of nerves, not collected in a bundle, running from the olfactory membrane in the nose to the olfactory bulb.

II. The **optic nerve** (afferent) is composed principally of axons from the ganglion cells in the retina of the eye. These pass back to the 'optic chiasm', where the fibers from the left half of the eye continue in the left optic tract, and the fibers from the right half, in the right optic tract, back to the external geniculate body, the pulvinar of the thalamus, and the superior corpora quadrigemina. From the first two of these **primary visual centers**, fibers pass to the visual cortex. From the third, fibers go to the **oculo-motor center**, which controls the contraction of the eye-muscles. Fibers also pass outward to the eye in the optic nerve from the primary centers. Some of these are from the oculo-motor center (just mentioned), but there are also fibers from the other two centers.

III. The **oculo-motor nerve** (afferent) arises from an extensive

nucleus lying along the front and central portion of the brain stem just above the pons (in the 'aqueduct of Sylvius' and the 'third ventricle'), emerging from the inner margin of the **crusta**. The cells in the anterior part of this nucleus send axons to the **intrinsic muscles** of the eyes (the *ciliary muscle* and the *sphincter pupillae*). The cells of the remainder of the nucleus send axons to certain **extrinsic muscles** of the eye, *viz.*, the *recti* (except the external rectus), the *inferior oblique*, and the *levator palpebrarum*.

Along with these axons, dendrites from cells in the nuclei are sent to the same muscles. These afferent neurons, whose cell bodies are located in the same ganglia with the bodies of efferent neurons, with the distribution of whose axons the distribution of the dendrites is coextensive, are called **proprioceptive** neurons.

IV. The **trochlear** or **pathetic nerve** (efferent and afferent) arises from a nucleus behind that of the third nerve, in the floor of the aqueduct of Sylvius at the level of the inferior corpora quadrigemina. The fibers emerge through the *valve of Vieussens* (the thin plate which forms part of the anterior wall of the 'fourth ventricle' in front of the cerebellum). The axons forming this nerve run to the *superior oblique* muscle of the eye.

V. The **trigeminal** or **trifacial nerve** (afferent and efferent) corresponds to a spinal nerve, having afferent fibers from cells in the 'Gasserian ganglion', which send their axons into the pons, and efferent fibers arising from nuclei in the lateral walls of the fourth ventricle and higher in the brain stem. The afferent axons branch, like the fibers of spinal nerves, the ascending branches going to a nucleus in the upper part of the pons, the descending branches passing forward as far as the cervical part of the spinal cord.

The afferent dendrites run to the face, including mouth, eye-balls, and nose. The efferent axons run to the muscles of mastication, and the *tensor tympani* muscles of the ears and the *tensor palati*.

VI. The **abducent nerve** (afferent and efferent) arises from a nucleus of cells growing in the floor of the upper part of the fourth ventricle on each side of the middle line, emerging from the anterior side of the medulla at the lower edge of the pons. The axons of the sixth nerve run to the external rectus muscles of the eyes, and are accompanied by proprioceptive dendrites as in the case of the third and fourth nerves.⁹

⁹ The nuclei of the third, fourth, and sixth nerves receive collateral fibers ('commissural') from the posterior longitudinal bundle, many of which are axons from cells in 'Deiter's nucleus'. By means of these commissural fibers, doubtless, the actions of the various eye muscles are coördinated.

VII. The **facial nerve** (afferent and efferent) has its nucleus for efferent fibers in the medulla behind the superior olive, from which the fibers emerge somewhat above this point on the sides of the pons and run to the muscles of the face, scalp and external ear. The afferent dendrites originate in the 'geniculate ganglion', from which some of them run to certain of the gustatory organs in the tongue, and some probably to endings in the muscles supplied by the axon of this nerve (proprioceptive, therefore). These fibers leave the main nerve through the 'nerve of Wrisberg'. The afferent axons have ascending and descending branches like those of spinal nerves.

VIII. The **auditory nerve** (afferent) joins the medulla close to the outside of the seventh nerve. The nerve is composed of axons of bipolar cells in the cochlea (on the **cochlear branch**) and in the vestibule of the ear (on the **vestibular branch**). On entering the medulla, the axons from the cochlea division branch, the ascending branches terminating in the 'ventral' or 'accessory' nucleus, and the descending branches in the 'dorsal' or 'principal' nucleus (**acoustic tubercle**). From the nuclei new relays of axons cross upwards to the opposite sides of the medulla and run upwards in the **lateral fillets**, some being relayed in the **superior olivary nucleus**, and all terminating in the **posterior corpora quadrigemina** (and internal geniculate bodies?).

The fibers of the vestibular division of the eighth nerve also send their branches into the 'ventral' and 'dorsal' nuclei, the fibers, or at least many of them, running through the nuclei into the cerebellum, where they connect with cells in the 'roof' nucleus.

IX. The **glossopharyngeal nerve**; X. The **pneumogastric** or **vagus nerve**; and XI. The **spinal accessory nerve**, have their roots in a series of bundles in the sides of the medulla. The efferent axons of these nerves come from cells in the *dorsal nucleus* of the vagus and accessory nerves lying externally to the nucleus of the twelfth nerve (*hypoglossal nucleus*) (*v. infr.*) and from cells in the *nucleus ambiguus* which lies deeper in the medulla.

The axons of the ninth nerve run to the muscles of the pharynx and the base of the tongue, and to the *parotid* gland. The afferent dendrites originate in cells of the *ganglion petrosum* and *ganglion superius*, and run to the mucous membrane of the tongue, mouth and pharynx.

The efferent axons of the tenth nerve run to the *levator palati* and the three *constrictors* of the pharynx, the muscles of the *larynx*, the muscular walls of the esophagus, stomach and small intestine, certain smooth muscles in the walls of the bronchi and bronchioles, to the glands of the stomach and possibly to the pancreas. In addition, *inhibitory* fibers run

to the heart. The afferent axons of the spinal accessory (eleventh) nerve supply the *sterno-mastoid* and *trapezius* muscles.

XII. The **hypoglossal nerve** (efferent) arises from cells in the floor of the fourth ventricle at its lower end, close to the middle line, and issues from the front side of the medulla between the anterior pyramid and the 'olivary body'. The axons run to the tongue (anterior portions) and extrinsic muscles of the larynx, and those moving the 'hyoid' bone.

REFERENCES ON GROSS RELATIONS OF NERVE, CORD, BRAIN, AND GANGLIA.

Starling, *Physiology*, Ch. VII, §§ VI, X, XI, XV and XVIII.

Cunningham, *Anatomy*, § The Nervous System.

Villiger, *The Brain and Spinal Cord* (Piersol's Translation).

Schäfer, *Quain's Anatomy*, Vol. III, Pt. I (General Neurology and the Central Nervous System).

Howell, *Physiology*, Chs. VIII-XI.

Lewis and Stöhr, *Histology*, § III, Sub-§ The Central Nervous System.

CHAPTER VII.

THE VISCERAL OR SPLANCHNIC DIVISION OF THE NERVOUS SYSTEM.

UP to this point our discussion of nervous structures has been chiefly of those neurons whose bodies are located in the brain and cord, or which connect the brain or cord with striped muscle or the organs of external sense. These neurons, taken together, are properly said to constitute the **somatic** division of the nervous system. Sometimes this somatic division is designated as the **cerebro-spinal** system; a designation which is perniciously misleading, since the cerebro-spinal system (if the term is to be used at all), includes more than the somatic division; includes, in fact, all nervous tissue except the cells of the 'local' plexuses, described below.

Those neurons which supply afferent and efferent connections between the brain and cord and the viscera—the smooth-muscle tissues of the blood vessels, skin, alimentary canal, etc., and the glandular tissues—are collectively designated as the **visceral, splanchnic** or **autonomic** division of the nervous system. Frequently, the word 'division' is dropped out and the expressions 'splanchnic system' (or visceral or autonomic, etc.) and 'somatic system' are used. It is to be remembered, however, that the somatic and the greater part of the splanchnic divisions are really parts of the cerebro-spinal system. There is some confusion in the use of terms referring to the splanchnic system, and even in the classification of the parts of the total system. The terminology and classification herein are in accordance with Starling, who is a good authority to follow in this matter.

The distinguishing peculiarity of the visceral system of nerves, from the morphological point of view, is the fact that the connection between the brain-stem or spinal cord and the structures supplied by the nerve-fibers is a two-neuron connection. This is true at least of the efferent neurons. As regards the afferent, information seems to be lacking. Competent authorities agree that the afferent visceral neurons of the spinal roots have their cell bodies in the spinal ganglia, as do the peripheral afferent somatic neurons, but do not decide whether these neurons extend to the visceral periphery or connect synaptically in the ganglia with a second set of neurons, as do the efferent visceral neurons. The efferent neuron which has one termination (and usually its cell body) in the cord (or in the brain stem) has its other termination in a ganglion at a greater

or less distance from the cord or brain, and the fiber (from cord or brain-stem to ganglion) is called a **pre-ganglionic fiber**. From the ganglion

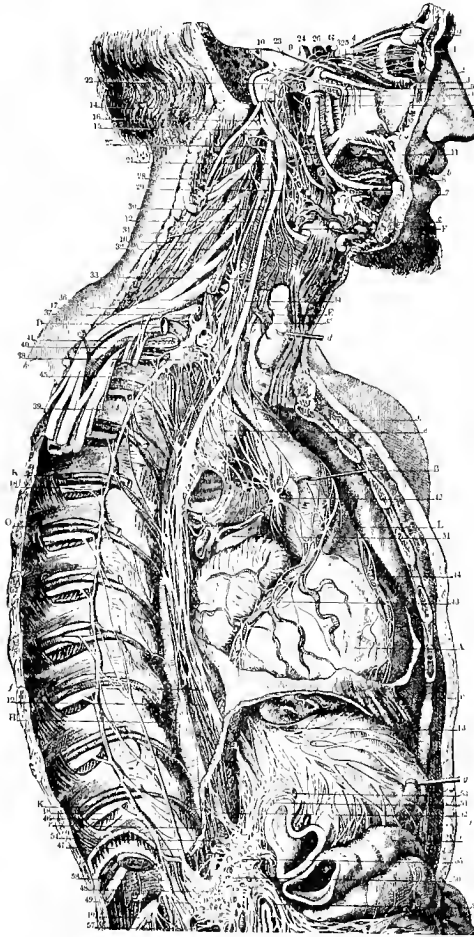


FIG. 72. The distribution and connections of the sympathetic and vagus nerves on the right side. (Quain's *Anatomy*, Vol. III, Pt. II, after Hirschfeld and Laveillé.) The sympathetic chain of ganglia is shown from the inferior cervical ganglion down to the first lumbar ganglion (58). *Ganglia*: 4, ciliary; 5, sphenopalatine; 6, otic; 7, submaxillary; 21, 33, 38, superior, middle and inferior cervical; 48, semi-lunar. *Glands*: *a*, lachrymal; *d*, thyroid. *A*, Heart. *g*, Stomach. 28, *Vagus* nerve. 47, *Great splanchnic* nerve. *Plexuses*: 42, cardiac; 50, solar; 53, gastric.

the connection with the smooth muscle or gland is completed by an axon or dendrite of a second neuron, called a **post-ganglionic fiber**.

The visceral division comprises several subdivisions, which may be grouped under these heads. 1. The **sympathetic division** (or system), so called because it was formerly believed to be capable of reflexes independent of the cerebro-spinal mechanism. 2. The **vagal, cranial, and sacral nerves and ganglia**. 3. The '**local**' systems of the alimentary canal.

1. The **sympathetic division** comprises the **sympathetic chains** of ganglia, one chain lying on each side of the vertebral column; and the **collateral ganglia** in special relation to the abdominal viscera. There is (on each side) one sympathetic ganglion for each of the spinal nerve roots from the fifth thoracic to the third sacral; there is one ganglion (the 'stellate' ganglion) connected with the first four thoracic roots, and two ganglia (the 'inferior and superior cervical') associated with the eight cervical roots.

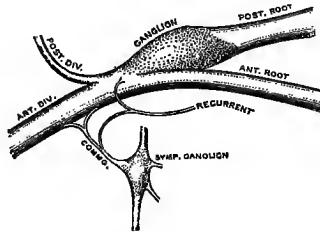


FIG. 73. The connection of a spinal nerve with a ganglion of the sympathetic chain. (*Quain's Anatomy*.) The two rami connecting the sympathetic ganglion with the spinal nerve are shown, and also the two roots of the recurrent nerve which supplies the tissues lying within the spinal canal surrounding the spinal cord.

There are three collateral ganglia lying near the points at which the large arteries originate from the aorta; these are the *superior mesenteric ganglion*, the *inferior mesenteric ganglion*, and the *semilunar*¹⁰ or *solar ganglion*.

The pre-ganglionic fibers of the sympathetic division leave the spinal nerves over the **white rami communicantes** of each nerve, and some of the post-ganglionic fibers are again given back over the **gray rami** to the spinal nerves for distribution to various parts of the body.¹¹ The white rami are largely composed of medullated fibers, and the gray rami are

¹⁰ Not to be confused with the *Gasserian ganglion* (cranial), which unfortunately is also called the *semilunar ganglion*.

¹¹ The majority of the post-ganglionic fibers of the 'sympathetic' division do not return to the spinal nerves, but emerge through the visceral nerves.

largely composed of non-medullated fibers; hence the difference in color. The pre-ganglionic fibers do not necessarily terminate in the ganglia nearest to the white rami over which they run. Some fibers pass up or down the chain to other lateral ganglia, and others run through to the collateral ganglia.¹² The post-ganglionic fibers given back to a spinal nerve through

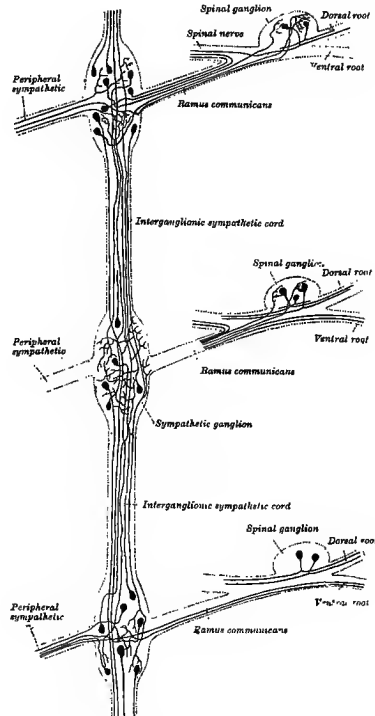


FIG. 74. Diagram of the motor connections of the sympathetic chain. (Quain's *Anatomy*, after Van Gehuchten.)

its gray ramus are connected with the pre-ganglionic fibers of a number of white rami.

The distribution of the post-ganglionic sympathetic fibers and the spinal origin of the pre-ganglionic fibers with which they are connected may be indicated briefly.

The first five thoracic nerve-roots, chiefly the second and third, supply the head and neck by way of the 'superior cervical' ganglion, and the

¹² Some fibers run through both lateral and collateral ganglia, terminating in peripheral ganglia (or terminal ganglia) in close relation to the organs supplied.

heart and lungs through the stellate ganglion. The lower thoracic and upper three or four lumbar spinal roots supply the abdominal viscera (stomach, small intestine, kidney, spleen), by way principally of the 'collateral' ganglia; and the colon, bladder, and genital organs by way of the 'pelvic' ganglia. The arm is innervated from the thoracic roots from the fourth to the tenth, through the 'stellate' ganglion; and the leg is supplied from the roots from the thoracic dorsal to the third lumbar, through lateral ganglia of the lumbar and sacral regions.

The functions of the 'sympathetic' nerves are, in brief: to cause contraction and relaxation of the muscular coats of the blood vessels (which functions are called **vaso-constrictor** and **vaso-dilator** respectively); to cause contraction and relaxation of the smooth muscle of various other viscera (**motor** and **inhibitory** functions); to stimulate secretion of salivary and sweat gland; and to accelerate the heart beat.

2. Visceral neurons of the **cranial, vagus, and sacral divisions.**

The third, seventh, ninth, tenth and eleventh cranial nerves contain visceral fibers, as well as somatic fibers. The visceral fibers in the third nerve are axons which run to the 'ciliary' ganglion in the orbit (eye socket) from which the impulses are relayed to the ciliary muscle (the muscle of accommodation) and the sphincter pupillae (muscle of the iris). The visceral fibers in the facial (seventh) nerve are efferent, but are dendrites of cell bodies lying in several cranial ganglia ('submaxillary', 'spheno-palatine' ganglia, *etc.*), differing thus from the typical arrangement of the efferent neurons conducting from the cord and brain. The fibres relaying from these ganglia terminate in the sublingual and submaxillary glands (salivary), the blood vessels of the tongue and the glands of various parts of the mucous membrane of the nose and mouth cavities.

The visceral fibers in the glossopharyngeal (ninth) nerve are axons and dendrites of cell-bodies in the medulla, and run to the *otic ganglion*, whence the efferent fibers are relayed by post-ganglionic axons to the parotid gland (salivary). Possibly there are ninth-nerve fibers running to blood vessels in the back part of the tongue. The tenth nerve, with some of the fibers derived from the roots of the eleventh, together form the **vagus**, or **pneumogastric** nerve, which, like the ninth nerve, is entirely visceral, and both afferent and efferent. The afferent fibers are dendrites derived from the 'jugular' ganglion, and the ganglion 'trunci vagi' (vagus trunk ganglion); the efferent fibers are (like those of the seventh nerve) dendrites of cell-bodies in the ganglia located in the viscera the nerve supplies. The efferent distribution of the vagus is to the smooth muscles of the gullet, stomach, small intestine, and bronchial

tubes; to the gastric glands of the stomach, and possibly of the pancreas; and to the heart. The effect of vagus currents on the heart is solely inhibitory, *i. e.*, decreasing the activity of the cardiac muscle. The distribution of the afferent fibers is not so clearly known.

The pelvic or sacral visceral connections of the central nervous system all run in the **pelvic visceral nerve** (*nervus erigens*), and are axons of spinal cell-bodies. These fibers terminate in the pelvic ganglia, lying in the neighborhood of the bladder, from which the further connections are with the muscles of the bladder, colon, rectum and sexual organs (and the blood vessels therein).

3. Local nervous systems.

The neurons described under 1 and 2 belong definitely to the central nervous system, as will be explained below. There are, however, certain groups of neurons which have not such direct connection with the cerebro-spinal apparatus. These are the **plexuses of Auerbach** and of **Meissner**, located in the walls of the alimentary canal from esophagus to rectum, and serving as 'centers' for this series of organs. They form, in other words, an independent local system, with afferent and efferent fibers having (probably) no communication with the general nerve system. Stimulation of the sensory terminals of neurons in this local system may therefore be transmitted by a relatively short circuit to the smooth muscle of the coats of the gullet, stomach, and intestines.

GANGLIA OF THE VISCERAL SYSTEM AND THEIR FUNCTIONS.

Ignoring now the local visceral systems just described, we find that the visceral system of neurons involves, in addition to the structures in the spinal cord and the spinal ganglia, two sets of ganglia. 1. The chain of lateral ganglia, and the collateral ganglia, of the 'sympathetic' division; and 2, certain peripheral ganglia (*i. e.*, ganglia located at a greater or less distance from the cerebro-spinal apparatus) of the cranial, sacral, and vagus visceral nerves. Among peripheral ganglia, for instance, are the otic, orbital, submaxillary, and pelvic ganglia earlier mentioned. These ganglia are sometimes called 'nerve centers', and properly come under one of the several meanings of that highly confusing term. But they are not (and this is important), structures in which afferent currents are converted into efferent currents. No reflex, in other words, can take place through these ganglia alone; the afferent current must go on into the cord, even if it does not go up to the brain, before it can be redirected outward to any of the effectors. The ganglia of the visceral nerves have merely a distributory function. A current passing out from the spinal cord in an axon which leaves the spinal nerve over the white ramus, is distributed,

in one of the lateral or collateral ganglia, to a number of cells therein, and its distribution in the tissues reached by the axons of these cells thereby increased. The current transmitted through a single white ramus is in many cases returned through the gray rami of many spinal nerves, and passes along fibers in the nerves to many portions of the body. It is not impossible that, conversely, afferent currents from a relatively large area may be collected in one of these ganglia by the dendritic branches of a single spinal ganglion cell. On this point, however, definite information is not at hand.

THE STIMULATION OF AFFERENT VISCERAL NEURONS.

The excitability of the afferent neuron terminations in the walls of the alimentary canal, especially the terminations of the visceral afferent neurons belonging to the central nervous system, has long been a subject for study and speculation. For a long time it was believed that these terminations, at least those below the gullet, although *afferent* were not *sensory*, *i. e.*, that no consciousness could be produced or mediated through their activity. It was shown that no specific sensations were experienced by a patient when his intestines were handled, pressed upon, cut, electrically stimulated, or even torn or burned. The peritoneal membranes covering the intestine, and lining the abdominal cavity, were found sensitive in one particular, *i. e.*, 'pain' was produced by strong stimulation; but no consciousness seemed to follow any operation on the intestines themselves.

The pain of colic and other less acute discomfort localized in the abdominal cavity were concluded to be due to peritoneal irritation.

Later and more adequate experiments have shown, however, that certain afferent currents from the intestines do produce consciousness, but that these afferent currents are initiated only when the nerve terminals are stimulated *adequately*, that is, in this case, when the intestinal muscular fibers are contracted or stretched. Thus we derive the experiences of pain (as of colic). Hunger is due to contraction of the stomach; fullness to stretching of the stomach walls, and probably feelings of 'faintness' and satisfaction, and others not readily named, are due to other variations in the stimulation of these organs.

Terminals of the local systems (of Auerbach and Meissner) are excitable through pressure of the contents of the canal on the lining membrane, and through the chemical substances contained in food, and in secretions of other regions of the canal. In this way the internal control of the digestive process is maintained. Whether afferent terminals belonging to the central system may be chemically stimulated is an open question. As to the stimulation of afferent visceral terminals in connection with tissues in

the skin, blood vessels and glands, and the specific effect thereof, we have yet all to learn.

REFERRED PAIN.

In certain pathological conditions of the visceral organs, the pain which is felt is falsely localized in the skin. This association of skin areas with visceral regions is definite and specific, and by the exact area of the skin which seems sore (although the skin is really normal), it is possible to diagnose the exact visceral region affected. The linkage of skin and viscera is doubtless through associative neurons located in the spinal ganglia. Such neurons have been discovered, and probably join cell-bodies of visceral neurons with cell-bodies of somatic neurons. In this way it would be possible for currents entering through the visceral channels to be switched off to the somatic neurons and continue upwards over that route, although the transfer does not occur unless there is pathological irritation.

REFERENCES ON THE VISCERAL DIVISION OF THE NERVOUS SYSTEM.

- Langley, The Sympathetic and Other Related Systems of Nerves. Schäfer's *Text-Book of Physiology*, Vol. II.
Starling, *Physiology*, Chapter VII, § XVIII.
Howell, *Physiology*, Chapter XII.
Herz, *The Sensibility of the Alimentary Canal*. London: Frowde, 1911.
Cannon and Washburn, An Explanation of Hunger, *American Journal of Physiology*, 1912, Vol. XXIX, pp. 441-454.
See also articles by Cannon and his pupils in the 1913 and 1914 number of the *American Journal of Physiology*.

CHAPTER VIII.

GLANDS.

GLANDS are organs of secretion or of excretion. In structure they involve all five fundamental bodily tissues—epithelial, connective and vascular in all cases, nervous tissue in nearly all, and muscular tissue in the larger glands—but the secreting or excreting agents in the glands are cells of epithelial origin.

Secretion is the production from the bodily fluids—or, in some cases, the mere separation from the bodily fluid—of substances which are directly useful to cells other than those secreting them, or which are useful to the organism as a whole: *e. g.*, saliva, produced by the salivary glands, is necessary for the digestion of starch; and sweat, produced by glands in the skin, helps to regulate the skin temperature. **Excretion** is the separation or the elimination from the bodily fluids of waste products of cells other than those excreting them: *e. g.*, urine, excreted by the kidneys. Sometimes a gland combines both functions, as in the case of the liver, the secretion of which (bile) both contains waste products and is also an important agent in intestinal digestion. The processes of secretion and excretion are, in a sense, common to all cells. All cells take up from the blood and lymph substances required for their own nutritive processes and give off waste products. But technically the terms 'excretion' and 'secretion' apply only to the processes as described above, *viz.*, in which certain specialized cells are carrying on the functions for the direct benefit of other cells.

There are many secreting cells—gland cells—which are not located in glands, but are scattered in epithelial membranes, especially in the mucous membrane. Such are the 'goblet cells', earlier described. Goblet cells, which, during their period of activity, form a mass of secretion within themselves and then liberate it at the end of the period of activity, represent the middle type of gland-cell. At one extreme are cells which probably produce and liberate their secretions continuously during the active period: such are the cells of the parotid gland. At the other extreme are cells which, having become filled with products during the active period, are themselves broken up, and mingle with their secretions in the process of discharging them; such are the lacteal cells in the mammary glands, and the cells of the sebaceous glands in the skin.

Glands are classified, according to their morphology, first, and in general, as **duct-glands** and **ductless glands**. The duct-glands are again classified as **simple** and **compound**, and also as **tubular**, **saccular** (or **alveolar**), and **solid**.

Ductless glands discharge their products directly into the blood stream, or into the lymph, so that the veins and lymphatic vessels draining these glands may be considered as also their ducts. The products of these glands are frequently designated as **internal secretions**, or more technically, **hormones**. Ductless glands are of course secretory only, and the secretion is clearly a process of manufacture, *i. e.*, the blood leaving these organs contains substances not contained in the entering blood. The practical use of these substances (hormones) is to excite or sensitize cells to which the blood stream carries them.

Duct-glands produce, or separate from the blood or lymph, substances which are needed for specific purposes outside of the body tissues, or of which the body needs to get rid. The ducts through which these glandular products are delivered to the proper points are therefore essentially separate from the other connections of the gland. The products of the duct-glands are commonly designated as **external secretions**.

DUCT-GLANDS.

The duct-glands are sometimes referred to as **true glands**; sometimes they are designated simply as **glands**; the intention in this case being that the term 'gland' shall always signify the duct-gland when not qualified by the adjective 'ductless'. These usages are due to the fact that the duct-glands were known and studied before it was known that the ductless glands are secretory organs also, and the term 'gland' has accordingly seemed to belong to the former alone. This terminology is needlessly conservative; the ductless glands are as truly secreting organs as the duct-glands and have as good a claim to the designation. It is unfortunate that we have not terms more easily distinguished than 'duct' and 'ductless': *cannulated glands* is a perfectly logical term for duct-glands, but it is not in use.

The simplest duct-gland is a pit or pocket in an epithelial surface, lined with secreting cells.¹³ This pit may be **tubular** in shape, whether straight or coiled, or may be **saccular (alveolar: acinous)**, *i. e.*, pouch-like, with its orifice smaller than its internal cavity. The sweat glands in the skin, and many of the gastric glands in the stomach, are tubular: the only

¹³ Many of the simple glands, and the small compound glands, although their duct-orifices open on epithelial surfaces, lie mainly in the connective-tissue layers below the epithelium.

simple saccular glands found in the human body are a few of the sebaceous glands of the skin. In **compound** glands the **lumen**, or inner part of the canal of the glands, is branched; in many glands the lumen branches repeatedly, so that the canal structure is very complex. Compound glands may be tubular, saccular, or **sacculo=tubular** (*acino-tubular*; *tubo-alveolar*). The compound saccular glands are often designated as **racemose** glands. The kidneys and the majority of the gastric glands are compound tubular. The *salivary glands* ¹⁴ and most of the sebaceous glands of the skin, the *Meibomian* (or *tarsal*) *glands* in the edges of the eye-lid, and the *mucous glands* in the oral, nasal and respiratory passages are compound saccular.

The **pancreas**, and **Brunner's glands** in the small intestine, are types of compound sacculo-tubular glands. The acini (sacs) in these glands are long and narrow like the lumen-branches of the compound tubular glands, but are distinguishably larger in diameter than the ducts into which they discharge.

The **liver** is a duct-gland, but it does not belong to either the saccular or tubular classes. In glands of these classes there is a cavity (tube or sacculle), or a number of cavities, connected with the same duct, and the secreting cells line these cavities. In the liver the secreting cells are arranged in solid masses (no cavities) and fine branches of the bile duct run everywhere between them. It is therefore classed as a **solid gland** (Cunningham).

The compound duct-glands are in most cases surrounded by **capsules** of connective tissue and from this connective tissue, if the gland is very complex, *septa* extend into the gland, dividing it into **lobes** and **lobules**. Each lobe or lobule contains sacculles or tubules opening into a common branch of the duct. The secreting cells in the case of the complex glands are confined to the sacculles or tubules, the cells of the epithelial lining of the duct proper being non-secreting. In the simple glands the entire lining of the cavity may be secretory, but usually in these also the secreting cells are confined to the deeper part or **fundus**, the more superficial portion being merely a duct.

The glands are all supplied with blood vessels and lymph vessels. Most glands are supplied with nerves, in some cases from both the autonomic and the direct cerebro-spinal systems.

Some of the gland nerve fibres run to the muscular cells of the blood vessels, some to the muscles of the ducts, and some to the secreting cells

¹⁴ According to Cunningham. Howell describes them as tubular; Pierson as tubo-alveolar.

themselves. The activity of a gland can be altered by nerve currents affecting the cells directly and by changes in the volume of the blood supply produced by contraction or enlargement of the blood vessels as well as by the influence of substances (such as CO_2 or the secretions of the ductless glands) brought to the gland cells in the blood.

THE GENERAL STRUCTURE OF THE ALIMENTARY CANAL.

The consecutive gross divisions of the alimentary canal are the **mouth cavity**, the **pharynx** or *throat*, the **esophagus** or *gullet*, the **stomach**, the **small intestine**, and the **large intestine**. The stomach connects with the gullet through the **esophageal orifice** and with the small intestine through the **pylorus**. The small intestine is divided into *duodenum*, *jejunum* and *ileum*, the first being the upper ten or eleven inches of the intestine and distinguished from the remainder both structurally and functionally. The large intestine is divided into *cæcum*, *colon*, and *rectum*.

The entire alimentary canal is lined with **mucous membrane**, consisting of a surface layer of stratified epithelium resting on a layer of connective tissue called the *stroma* or *tunica propria*, with sometimes a *basement membrane* separating the two. Beneath the mucous membrane are muscular and connective-tissue structures which, in the gullet, stomach and intestines, take on the form of definite coats.

The four coats of the gullet, stomach and intestines are therefore:

1. The **mucous membrane**. The lowest stratum of the stroma (in the organs mentioned: not in the mouth and pharynx) is a sheet of smooth muscle fibres.

2. The **submucosa**. This is a loosely attached layer of areolar connective tissue.

3. The **muscular coat**. In the upper part of the gullet this is composed of striated muscle; in the middle portion, of both smooth and striated fibers; in the lower portion of the gullet and throughout the stomach, small intestines, caecum and colon, there are smooth fibers only. In the gullet and intestines the muscle fibers are arranged in two layers, an inner *circular layer* and an outer *longitudinal layer*. In the stomach there are three layers.

4. Surrounding the muscular coat of the upper part of the gullet is a coat of areolar connective tissue loosely joining it to the adjacent structures. The lower part of the gullet, stomach and intestines have a serous coat of smooth connective tissue, the **peritoneum**, which is continuous with that lining the abdominal cavity. From the serous coat of the stomach folds of peritoneum called *omenta* (singular *omentum*) pass to the large intestine, to the liver, to the spleen, connecting the stomach with these

organs. Portions of the jejunal and ileac divisions of the small intestine are united to the abdominal wall by peritoneal folds called *mesenteries* which convey the nerves and blood vessels to the intestines.

GLANDS OF THE ALIMENTARY CANAL.

The principal glands opening into the human mouth-cavity are the three pairs of salivary glands, *viz.*, the **parotid**, the **submaxillary** and the **sublingual** glands. [Fig. 75.] These are compound alveolar in structure. Sometimes there are vestiges of a fourth pair, the *retrolingual*, which are fully developed in the dog, cat and pig. In addition the mucous membrane of the mouth, especially of the under side of the tongue, is full of small glands, mainly of the compound alveolar type. The mingled secretion of all of these glands is the **saliva** which normally contains desquamated epithelial cells, disintegrating leucocytes and gland cells, as well as inorganic salts and clots of mucus. The most important constituent of saliva is *diastase*: an enzyme which converts starch into sugar. The salivary digestive process begins in the mouth, and if the food be well mixed with saliva, continues for some time in the stomach, until stopped by the gastric juice, which penetrates slowly into the food-lump formed by the act of swallowing.

The secretory cells in these glands are of two types: *mucous cells* similar to the goblet cells already described, and *serous cells*, secreting a more watery substance. The secretory cells of the parotid are practically all of the serous type. The other glands are mixed, containing both serous and mucous cells. In the mucous membrane of the esophagus there are small glands similar in form to those of the oral cavity but of the pure mucous type.

The nerve fibers of the salivary glands come from both the vagus and the sympathetic division of the autonomic system. [The course of the salivary nerve fibers issuing from the vagus is complicated; probably all issue in the *nervus intermedius*. The fibers to the parotid glands pass by the glossopharyngeal nerve to the Vidian nerve and to the otic ganglion; from thence fibers run by a branch of the fifth nerve to the gland. The fibers destined to the sublingual and the submaxillary glands run in the facial nerve to the lingual through the *chorda tympani*, and end on ganglion cells near the glands, from which fibers run to the secretory cells. The sympathetic fibers issue from the three upper dorsal nerve-roots, pass through the stellate ganglion, and are relayed in the superior cervical ganglion. From here the fibers follow branches of the external carotid arteries to the glands.]

The vagal nerve fibers excite the secretory cells directly and also

cause dilation of the arterioles in the glands and hence increased blood supply. The effects of currents in the sympathetic fibers are not clearly marked, but include vasoconstriction. Apparently the activity of the salivary glands is controlled entirely by nerve action. Secre-

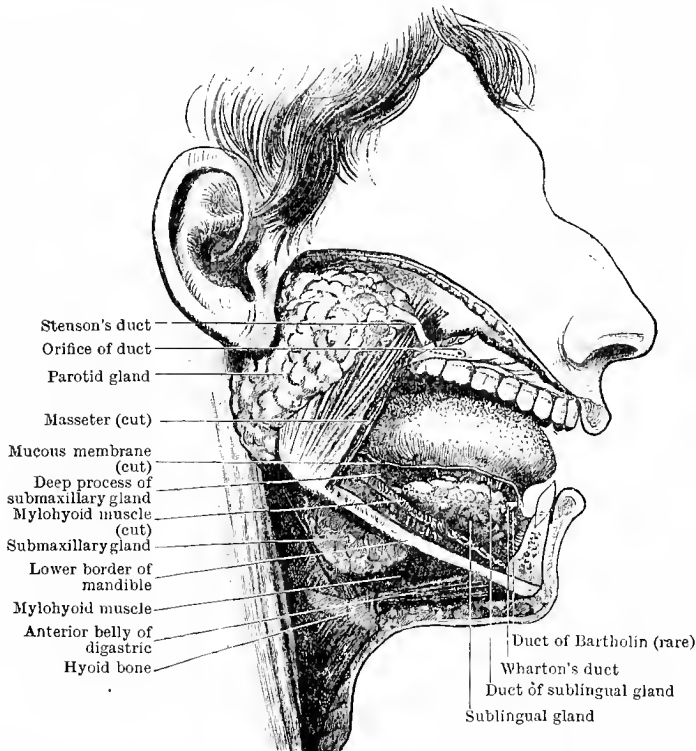


FIG. 75. The Salivary glands and their ducts. (After Cunningham.) The greater portion of the lower jaw and part of the masseter muscle have been removed to show the sublingual gland and the lower part of the submaxillary gland. Four ducts of the sublingual gland are shown, opening on the floor of the mouth, and a fifth (duct of Bartholin) opening into Wharton's duct. Wharton's duct and Stenson's duct are the drains of the submaxillary and parotid glands respectively.

tion is normally started by the tact and taste of food within the mouth and by the smell and sight of food. Reflex habits may easily be built on arbitrary stimuli, such as sounds. The ringing of a bell or the sounding of a tuning fork or the sight of a placard may be a salivary excitant for a dog as well as for a man.

Salivary reflexes may be studied in the human subject by inserting a cannula¹⁵ in the duct orifice of the submaxillary or parotid glands, thus collecting saliva so that its quantity and constitution as well as the time of its appearance may be noted. In work on animals which has been carried on extensively by the Russian Pavloff¹⁶ and his students, De Graff's method has been followed. De Graff's method consists in transplanting

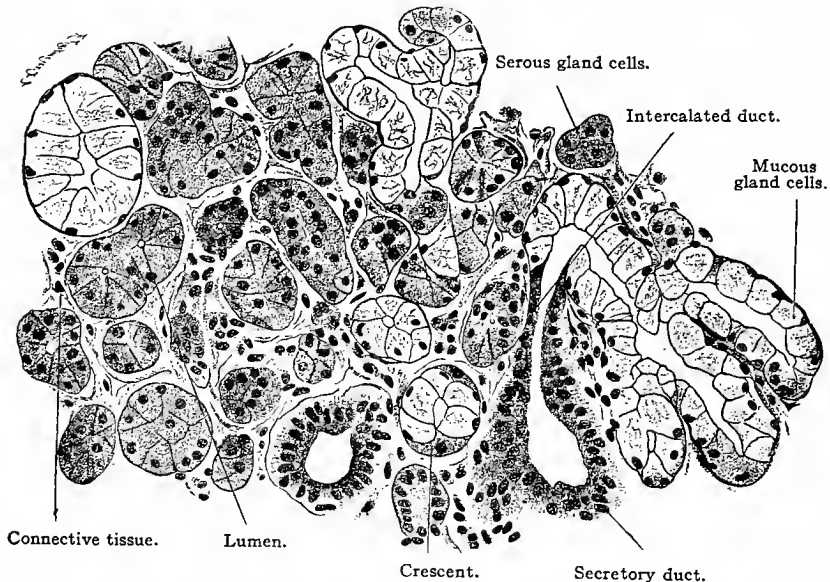


FIG. 76. Section of submaxillary gland of an adult man. Magnified 252 diameters. (Lewis and Stöhr, *Histology*.)

the orifice of one of the salivary ducts to the outside of the face, thus making a *salivary fistula* so that the secretion can readily be collected with minimal discomfort to the animal.

The glands of the stomach, which secrete gastric juice, are tubular, some being simple, but the majority compound. There are three types of these glands: the *fundus*, the *cardiac* and the *pyloric* glands. The fundus

¹⁵ The cannula is a tube of metal, rubber, or some other hard substance.

¹⁶ Pavloff's name is frequently and inconsistently spelled by English writers after the German fashion, Pawlow. The inconsistency lies in using the German instead of the English transliteration of the Russian name. As we can not conveniently use the Russian spelling, we should use, in English, the English spelling. The French rendering is Pavlov.

glands, which occur throughout the greater part of the stomach, are simple, or else have few branches. The pyloric glands, which are larger than the fundus glands, occur in the part (about one-fifth) of the stomach nearest the pylorus. The cardiac glands are situated only in a narrow ring near the esophageal orifice: they resemble the fundus glands in size but are complex like the pyloric glands. In these glands there are two kinds of cells, *chief cells*, secreting the digestive enzymes (pepsin and rennet), and *parietal cells*, secreting hydrochloric acid. The pyloric glands contain only chief cells; the other gastric glands contain both kinds of cells. These glands are supplied with nerve fibers derived from both the sympathetic and vagal divisions of the visceral nervous system, the immediate supply being from the solar plexus. There are also two local nerve systems in the stomach as well as in the walls of the intestines: the **plexus of Auerbach** in the muscular coat, and the **plexus of Meissner** in the submucosa. These plexuses contain numerous ganglion cells and are possibly connected with fibers from the other parts of the autonomic system.

The gastric glands are excited to activity primarily by the same stimuli (visual, olfactory, tactual, etc.) which excite the salivary glands. The process of gastric secretion has therefore usually been started before the food enters the stomach, although there is a latent period of several minutes before the actual appearance of the juice. Contact with or pressure on the lining of the stomach itself has no effect. By making a gastric fistula and also a fistula in the esophagus, Pavloff proved that the secretion could be produced by the chewing and swallowing of food, or even by the sight of it, although no food entered the stomach.

Gastric secretion is also excited by the presence of partly digested food in the stomach. This stimulation may be due to the action of substances in the food, or substances (hormones) produced by the glands near the pylorus, acting on the local nervous systems. The greatest experts on the physiology of the internal organs (*e. g.*, Starling), incline, however, to think that the excitation is due to hormones which act directly on the gland cells.

The intestines are provided with glands of several types. In the walls of both intestines there are many simple tubular glands, **Lieberkuhn's glands**; and in the upper part of the duodenum **Brunner's glands** (sometimes described as compound-tubular, sometimes as acino-tubular), are plentiful, becoming less numerous below, and being entirely absent at the lower end of the duodenum. Whether the secretions of Brunner's glands and Lieberkühn's glands in the small intestines differ is not decided. In conjunction, these glands produce **intestinal juice** (*succus entericus*). The Lieberkühn's glands in the large intestine produce a dif-

ferent secretion; consisting principally of mucus for lubrication, and possibly containing excreted material. The two most important glands of the body,—the liver and the pancreas,—discharge their secretions into the upper end of the small intestine. The glands of the intestines are excited to activity by pressure on the intestinal lining and also by a hormone called **secretin** which, it is believed, is formed by the epithelial cells of the upper part of the small intestine, under the influence of the acid *chyme* (product of stomach digestion). The intestines are supplied with nerves from the sympathetic, the vagus and (in the case of the large intestine, at least) from the sacral division of the autonomic system, and contain plexuses of Auerbach and Meissner. There is not much information available, however, concerning the nervous control of the glands. The glandular response to pressure is probably a reflex from the local nervous system. There are indications that the fibers from the vagus have an inhibitory effect.

The **liver**, the largest gland in the body, has a weight in the adult in the neighborhood of 1600 grams (three and a half pounds). Its structure is very complex, consisting of numerous small masses (lobules) of secretory cells between which lie the branches of the **bile canaliculi** (corresponding to the tubules or alveolae of an ordinary gland), and amongst which run networks of blood vessels and lymph vessels. In its development the liver resembles a compound tubular gland, but the tubules anastomose with one another, forming an intricate network, and thus losing the characteristic tubular gland form. Instead of tubes whose walls are formed of numerous secreting cells, the canaliculi are minute passages between the solidly grouped cells, so that at most points the canaliculus wall is formed by the surfaces of only two cells. The intralobular network in each lobule opens externally into an interlobular **bile duct** which in turn opens into a larger duct, these ducts finally uniting to form the **hepatic duct**. From the hepatic duct, the bile is discharged through the **cystic duct** into the **gall bladder** between periods of intestinal digestion, but during digestion it passes from both the hepatic duct and the cystic duct through the **common bile duct** into the small intestine. The gall bladder has a muscular coat and there are numerous bundles of smooth muscle fibers in the walls of the hepatic duct and the bile ducts, the fibers being especially numerous at the orifice into the intestine.

The **pancreas** is a relatively large gland weighing about 86 grams (3 ounces) and lying behind the stomach. In form it is sacculo-tubular, *i. e.*, the terminal sacs are elongated, giving a cylindrical shape. In the human body the main duct of the pancreas (the **duct of Wirsung**) and the common bile duct empty into the duodenum through the same orifice. The

walls of the pancreatic duct contain smooth muscle fibers. Sometimes there is a secondary pancreatic duct.

Both the liver and the pancreas are supplied with nerve fibers from the solar plexus. Most of the fibers are sympathetic, but apparently there are some derived from the vagus nerve. Some of these fibers run to the muscular coats of the blood vessels and the ducts of the glands, and some run to the gland cells themselves. The details of nervous control of the liver and pancreas are obscure. The liver secretes continuously, but more copiously during digestion; the principal stimulus to the activity of both liver and pancreas has been shown to be the secretin manufactured by the small intestine, carried in the blood to the glands and acting directly on the gland cells. The same hormone also causes contraction of the gall bladder, emptying its contents through the common bile duct.

GLANDS OF THE SKIN. .

The chief skin glands are the **sweat glands** (*sudoriparous* or *sudoriferous* glands) and the **sebaceous glands** [Fig. 57]. The former are coiled simple tubes, the latter are alveolar.

The **sebaceous glands** are usually associated with hair, the ducts of one to four glands opening into the superficial part of the hair follicle. On some part of the body (the lips, for example), the glands open on the surface independently of the hairs. The active cells in these glands secrete by forming **sebum** within themselves and then liberating it by breaking down; new cells from the deeper layer replacing the dissolved ones. There are no nerve fibers supplied to these glands and no muscular fibers in the glands themselves. The contraction of the *arrector pili* muscle attached to a hair follicle (raising the hair follicle and thus producing the condition known as "goose flesh") compresses the sebaceous gland and squeezes out the sebum. These muscles are controlled by fibers from the sympathetic division of the nervous system.

The **sweat glands** are under the direct control of the sympathetic nerve fibers which terminate both on the secreting cells lining the tube and the smooth muscle fibers which lie next to these cells. These secretory nerve fibers are derived from spinal nerve roots from the second dorsal to the third or fourth lumbar. The normal stimulus for the sweat-reflex is heat applied to the surface of the body through external sources, or an increase in the temperature of the blood within the body. Concerning the mechanism of the excitation of the afferent currents which control the efferent current to the sweat glands, there is meager information.

The above list does not include all the duct glands, nor even all the important ones, but is sufficiently extended to give an elementary idea of the general facts of duct-gland structure and function.

THE DUCTLESS GLANDS.

Internal secretion is the production of **hormones**; substances which certain cells discharge into the blood, and which are carried by the blood stream to other cells, upon which these substances exercise a specific action. A certain hormone (**secretin**) we have seen is produced by epithelial cells in the duodenum; others are probably produced by cells in the epithelium elsewhere, and possibly by muscle cells.¹⁷ Certain glands, as for example, the pancreas, produce both an external secretion and an internal secretion: the hormone produced by the pancreas has a definite effect on nutritive processes throughout the body.

There is one class of glands conventionally designated as **ductless glands**, which produce internal secretions only. The principal members of this class are: the two **adrenal glands** (*suprarenal capsules* or *adrenal bodies*) lying near the upper end of the kidneys; the **thyroid** (or *thyreoid*) **gland** (or **body**) which partly surrounds the upper part of the trachea (windpipe) and the pharynx [Fig. 77]; the **parathyroid** (or *parathyreoid*) **glands** of which there are usually two pair lying near the thyroid; the **pituitary body** (*hypophysis*) lying in front of the brain stem [Figs. 66 and 67]; the **pineal gland** (or *body*) just above the corpora quadrigemina; the **carotid body**, at the bifurcation of the carotid artery; the **coccygeal body**, in front of the tip of the cocyx (the terminal vertebrae of the spinal column) [Figs. 29, 38]; and the **thymus** [Fig. 77] in the lower part of the neck and upper part of the thorax.¹⁸

The **thyroid**, the **parathyroid**, and in part the **pituitary body** have alveolar structure: *i. e.*, they contain lumina or follicles whose walls are composed of secreting cells; but these follicles have no ducts. The other ductless glands are rather of the solid type: the cells being bunched in masses or columns between which the blood vessels and lymphatic vessels ramify. The mechanism by which the hormones enter the blood—whether directly or through the lymphatic channels—is not yet definitely known.

All of these ductless glands are supplied with nerves which apparently are mostly from the sympathetic system, although there are also fibers

¹⁷ According to Howell, the liver cells produce two internal secretions—glycogen and urea. The former is conveyed to and consumed by muscle cells throughout the body; the latter is excreted by the kidneys. These substances, according to Starling, do not properly fall in the class of hormones; hormones are strictly substances which have a *stimulating* or *sensitizing* effect, as the derivation of the term *hormones* indicates.

¹⁸ The ovaries, testicles, spleen, and the lymph-nodes are sometimes classed as ductless glands. It is probable that these bodies produce hormones, but if so they are not their principal products.

from the vagus, cervical and sacral autonomic nerves. The nerve supply to the adrenal glands is so rich that these organs have formerly been supposed to belong to the sympathetic nervous system. Some of the nerve fibers terminate in connection with the blood vessels, and some in connec-

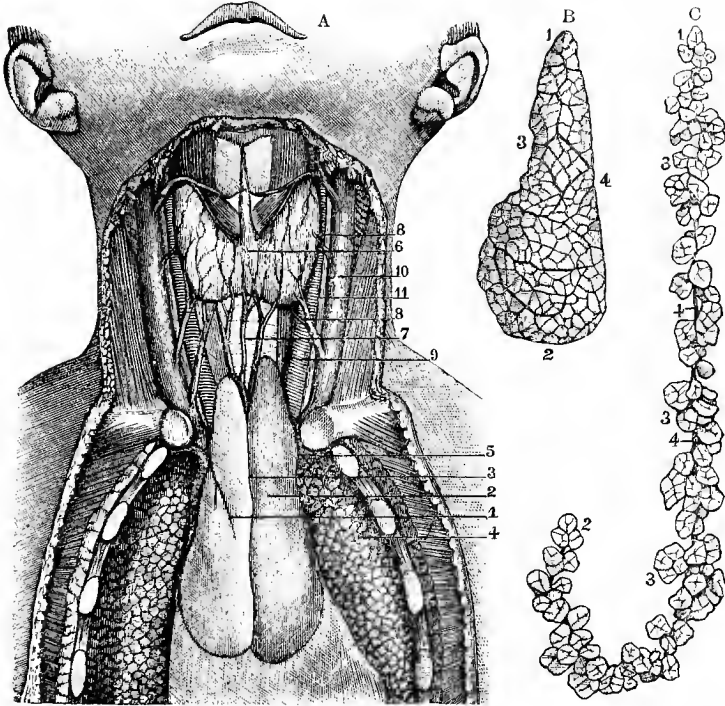


FIG. 77. The thyroid and thymus glands in a child of six months. (Schäfer, *Microscopic Anatomy*, after Sappey.) *A*. The positions of the thyroid and thymus glands: 1, 2, and 3, right and left lobes and median fissure of the thymus; 6, thyroid; 9, common carotid artery; 10, internal jugular vein; 5, 7, and 8, veins. *B*. Right lobe of thymus, with envelope removed. *C*. The lobe, unraveled, showing the strand of connective tissue along which the lobules are grouped.

tion with the secreting cells. Whether there are any sensory fibers is not known.

The secretion of the **thyroid** gland has an important influence on the growth of all the bodily tissues. In cases of removal of the thyroid gland a condition known as *myxedema* ensues; the metabolic processes proceed slowly; growth, except of connective tissue, stops; and death may follow.

In children, atrophy of the thyroid gland produces the state of arrested development known as *cretinism*. Cases of cretinism and myxedema may be relieved by feeding the patient fresh or dried thyroid glands of animals. The hypertrophy, or excessive growth of the thyroid, known as *goiter*, is productive of nervous irritability and muscular weakness. The function of the parathyroids is somewhat in dispute. In the view of some experimenters they are similar in nature to the thyroid, and if the latter be removed without injuring the former they can to a certain extent fulfill the latter's function. This theory is probably wrong.

The **pituitary body** consists of two *lobes*, *anterior* and *posterior*, with a *pars intermedia* between. The posterior lobe seems to have no secretory function. The secretion of the anterior lobe seems to promote growth, especially of the bones and connective tissue. The condition known as *acromegaly* or *gigantism*, in which the bodily frame grows to excessive size, are thought to be due to over-development or over-activity of this lobe. The secretion of the *pars intermedia* has an exciting effect on smooth muscle and on the gland-cells of the kidneys. Removal of the entire pituitary body causes death.

Of the functions of the other ductless glands little is known. The **thymus**, which enlarges during the first two years of life and then diminishes so that at puberty it is insignificant, probably has a specific influence on the growth of the child. The **pineal body** is glandular only during childhood, becoming a mere fibrous body at adolescence. Its secretion probably retards the development of the body, especially the development of the reproductive organs. The secretion of the **adrenal glands** (**adrenalin**, *suprarenalin* or *epinephrin*) has a marked effect on smooth muscle and gland cells, producing the same activity in these organs as is produced by stimulating the nerves supplying them. Removal of the adrenal bodies always causes death in from twelve to twenty-four hours.

Cannon has shown that the secretion of adrenalin is increased in animals under the influence of stimulations producing such emotions as fear or rage. The importance of the secretion in such circumstances can readily be understood, since it acts as a stimulant to the muscles and other organs and in particular increases the liberation of glycogen from the liver into the blood, and thus increases the energy-supply to the muscles. The effect of adrenalin on the digestive process is marked. It checks both the secretion of the digestive juices and also the muscular activity of the alimentary canal. It has long been known that certain strong emotions, especially fear and rage, are accompanied or followed by important changes in the digestive process, and the study of adrenalin is now revealing a part of the mechanism of the occurrences. On the physiological side, the research

of Cannon and his pupils opens up what is probably the most important line of attack on the problems of the emotions.

The foregoing sketch of the functions of the ductless glands should be taken as a statement of probabilities. There is serious conflict of opinion and conflict of apparent experimental results concerning these organs. At the present time an enormous amount of work is being done in this field by the physiologists, and the results of their researches will some time be of great value to psychology.

The psychological importance of the ductless glands does not lie simply in the fact that they are essential to the growth, nutrition and irritability of the muscular, glandular and nervous tissues, but in the connection which seems to exist between internal secretion and affective content of consciousness. Although we have as yet no data indicating clearly whether the hormones have a neural stimulatory value, exciting end-organs of afferent fibers in the viscera, or whether the consciousness factor is associated merely with the nerve reflexes which terminate in the activation of the glands, it is probable that the physiological basis of affective content will be found to be partly in some phase or phases of secretion.

The physiological basis of feeling is doubtless wider than internal secretion. On the one hand the nerve fibers activating the duct-glands are at least as important as those activating the ductless glands. On the other hand, if there are nerve receptors which are stimulated by hormones there are also probably receptors stimulated by other bodily products, such as carbon dioxide, lactic acid, and glycogen. Moreover, the activity of smooth muscle (aside from the smooth muscle involved in certain of the glands) probably plays some part in the physiological conditioning of affective contents and consciousness.

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CHAPTER IX.

THE FUNCTIONAL INTERRELATION OF RECEPTORS, NEURONS, AND EFFECTORS.

THE human body is a mechanism for producing **response** to stimulation. Response is always the modification of the activity of muscles or glands, or of both. Other activities in the body (such as the activities of blood corpuscles) are subsidiary to these responses, modifying their character, temporal course, or extent.

The responses of a muscle or gland are of two kinds: increase in activity, or decrease in activity. In the muscle the increase in activity is manifested in **contraction**; the decrease, in **relaxation**. In the gland, the activity which is subject to increase and decrease is **secretion**, that is, the formation, or separation, of some substance or substances (saliva, mucous, sweat, adrenalin, etc.) to the elaboration of which the gland is especially adapted.

Striped muscle contracts normally only when irritated by a nerve current (excitatory or acceleratory current). Relaxation supervenes on contraction when the exciting current ceases, but is also facilitated by nerve currents. These latter currents are called *inhibitory*. Whether there are two specifically different classes of efferent neurons, one class having acceleratory effects, and the other inhibitory effects; or whether two branches of the same axon may have contrary effects (on two different groups of muscle fibers), has not been made clear.

In distinction from the production of positive contractions, acceleratory nerve impulses to muscles may have a *tonic* effect (may give *tone* to the muscles). Tone in a muscle is a condition of preparedness for contraction, and may be called the normal condition of muscle. If the efferent nerves supplying a muscle are completely severed, the muscle becomes flabby, and much greater stimulus (*e. g.*, electricity applied directly to the muscle or to the cut end of the nerve) is required to produce contraction than is required in the case of muscle having tone.

The unstriped and cardiac muscle also receives tone through nerve currents. In the normal body, therefore, there is a constant flow of acceleratory current through the efferent nerve fibers to the general musculature, keeping it in condition for action.

Chemical substances carried by the blood to muscles are also an important factor in the maintenance of tone. An increase, for example, in the quantity of adrenalin, secreted into the blood from the supra-renal glands, heightens the general muscular tone. This effect is not considered, however, as a direct tonic effect, but as a sensitizing of the muscle, so that the nerve currents produce relatively greater effect.

Smooth muscle, whether in the intestines, blood vessels, skin, or elsewhere is in general subject to the same laws of stimulation as is striped muscle. It seems, however, to be excited by other than nerve action, and in particular, contraction of certain fibers may stimulate adjacent fibers. There remains, however, some uncertainty on this point, as also on the points concerning the causation of the rhythmic contraction and relaxation of cardiac muscle.

The acceleration and inhibition of glandular activity is brought about by nervous activity both directly and indirectly. Directly, the nerve currents conveyed to the gland cells seem to stimulate them to greater activity, or to check their activity.¹⁹ Indirectly, currents to the muscular coats of the arteries supplying the glands, by dilating and contracting the arteries and therefore increasing or decreasing the blood supply, increases or decreases the glandular activity, since the material for the secretion is derived from the blood.

The important bodily activity, in short, is muscle and gland action, and this is to a large extent directed by the nervous system. The nervous system, on the other hand, is controlled by physical and chemical stimuli from objects external to it. *Efferent* currents control the effectors, but efferent currents are but the sequelae of afferent currents from the various receptors. The receptors, in turn, are excited to function by the action of: 1. Pressure on the receptor (certain receptors in skin, mucous membrane, and other tissues). 2. Light (retinal receptors). 3. Sound (cochlear ending). 4. Substances in solution (taste bud receptor and receptors in the alimentary canal). 5. Gaseous substances (olfactory cells). 6. Temperature changes (receptors undiscovered). 7. Muscular contraction (muscle spindle receptors and receptors in smooth muscle). The last form of stimulation is not identical with pressure, since the receptors in smooth muscle cannot be stimulated by pressing upon, pinching, or otherwise maltreating the tissue; but respond only to the contraction of the tissue.

¹⁹ Contraction of the muscle fibers in the ducts of a gland may play an important part in the pouring-out of the secretion. Thus, when an animal smells or sees food the saliva appears, through contraction of the ducts, before there is a significant increase in the secretion.

The human body is therefore, physiologically considered, but an exceedingly complicated machine, played upon by a great many external forces, and responding to these forces in such a way as to maintain its integrity for a considerable time and to produce other machines similar to itself. The physiological performance of such a machine may be summed up under two heads. 1. **Reflexes:** processes initiated by an external stimulus to a receptor and ending in modification of muscular and glandular activity. 2. Processes contributory to the reflexes. Under this last head go nutritive and similar chemical activities, and the activity of cells essential to the nutrition and protection of the reflex mechanism.

Physiology, however, does not exhaust our interest in the organism. It is true, so far as the organ alone is concerned, that when light strikes the eye, all that happens as a result thereof is the contraction of certain muscles, relaxation of certain others, acceleration of certain glandular activity and inhibition of certain others. But another thing also happens which is not to be found in the organism at all. If the eye be *my* eye, *I see* the light when this organic reflex occurs. Similarly I am aware of the sound which stimulates my ear, of the sweet which stimulates the taste buds; and of the contraction of the biceps which stimulates the spindles therein. Moreover, I am aware of the activities of my viscera through the operation of the reflexes in which these take part; an awareness which (in contradiction to the awareness of these operations which I might have through visual reflexes, for example, if my viscera were laid open for microscopic examination) I call 'having feelings'.

These awarenesses (which together we call **consciousness**) depend upon the action of reflexes. Without a reflex from the eye I cannot see light. Without reflexes from my viscera I cannot have 'feelings'. To say that the reflexes *cause* the consciousness is to make an extrascientific assumption which is not justified, unless we mean by 'cause' no more than *invariably accompany*.

The awarenesses just indicated are **perceptual**. In addition there is a form of consciousness which we call **thought**. I can think of red light, when the appropriate stimulus does not fall on the eye, and when therefore the perceptual light reflex does not occur. There is, in this case, doubtless a reflex, which, although not initiated in the same receptor as the perceptual light reflex, has the same termini as the latter. The initiation as well as the termination of one of these thought-reflexes is probably always the contraction of striped muscle. Thus, on this assumption, all forms of consciousness are concomitants of reflexes.

The important question now is: what sort of reflexes condition consciousness? The answer is: those which take place through the 'central

nervous system' (brain and cord). The reflexes through local ganglia (such as the ganglia in the walls of the alimentary canal, or in the heart), are to be excluded, as probably having no part in the conditioning of consciousness.

It is commonly supposed that only the reflexes which take place through the cortex are 'conscious'. In fact, it is often held that it is the action of cortical cells which is the ultimate condition of the consciousness. For this view there seems to be no strong evidence. For aught we know action of muscle may be the more essential part of the process, and it is safest for the present to make no attempt at localization within the total reaction process. We cannot even admit that it is essential for the production of consciousness that the arc (or path) of the reflex should lead through the cortex. A spinal reflex has all the essential conditions of consciousness, so far as we know. It would be rashly dogmatic even to say positively that the reflexes within the intestinal plexuses of Auerbach and Meissner do not condition consciousness.

In order to avoid confusion, the reader must here note that the term **reflex** is here used in the strict technical sense to designate the total process taking place over an arc; that is, the process beginning in an end-organ (such as the cone in the retina), passing along a series of neurons (arc) to the spinal cord, and in some cases from thence to the brain, and finally reaching some effector (muscle or gland cell), or effectors, whose activity is consequently modified. This process is called a 'reflex' because it may be thought of (in an untechnical way) as a process which is directed inward to the nerve center, and from thence *reflected* out again to the periphery.

Unfortunately the process in which a reflex terminates, which is properly called **reflex-action**, has come to be described by many writers by the shorter name 'reflex'. This is bad usage. The mere contraction of the iris, for example, when light is suddenly thrown into the eye, is a 'reflex contraction' but is not a 'reflex'. The 'reflex' is the total process beginning with the retinal activity produced by the light stimulus and terminating in the pupillary contraction.

Another source of confusion lies in the fact that formerly it was assumed that only a limited class of activities are the results of reflexes. 'Reflex action' was set over against 'voluntary action', and sometimes other forms of action were distinguished from these. The more modern view, which is adopted here, considers all normal actions as the termini of reflexes: it holds, for example, that voluntary actions, such as dropping a letter in the box after deliberating whether to post it or not, are just as much 'reflex actions' as are the blinking of the eye when a cinder strikes it, and the deep inhalation which follows the perception of a faint pleasant odor.

THE FUNCTIONAL UNITY OF THE CENTRAL NERVOUS SYSTEM.

Before considering further the dependence of consciousness on organic reflexes, it is necessary to look at the nervous system from the point of view of its mode of function.

An afferent impulse over a single neuron is capable of being transmitted to any efferent neuron of the centralized nervous system, including the visceral division (but excluding of course the local system: plexuses of Auerbach and Meissner), or to a large number of such neurons. That is to say: the irritation of an afferent neuron may, through the successive passing of the irritation to various intermediate (associative and commissural) neurons cause the irritation of any efferent neuron, or of a number of such neurons, and so may modify the activity of any muscle or gland, or of a large number of effectors.

Impulses are constantly passing inward over the afferent chains. Even in sleep, the only afferent neurons which suspend their activity are those from the retina, and from some of the striped muscles, and possibly from some small areas of the skin. The afferent terminals in smooth muscle, and in the muscles of the breathing mechanism, are still being stimulated, with about normal response. Conversely, there is a continuous and widely distributed outgo, maintaining the tone of the muscles, and stimulating or inhibiting contraction and secretion. Even in sleep, the control of the visceral organs, and of respiration, cannot be suspended, and the tone of the striped muscle generally must be maintained.

The neural mechanism, therefore, must not be regarded as a collection of potential or actual arcs, but as one enormously complicated arc, in which, for legitimate purposes of description we distinguish multitudinous paths from sensory periphery to motor periphery. These individual arcs are not fictitious, but are to a certain extent abstractions.

The following example of a reflex may make the relation of total system and particular function more clear. The organism may be so disposed that a stimulus to the eye produces a specific movement of the hand; this is the case in a simple reaction measurement when the reactor is instructed to press a rubber bulb immediately on seeing a light. In this case there is probably a discharge through a series of neurons running from the retina of the eye through the mid-brain (and possibly through the cerebral cortex), down the spinal cord, and out through the spinal root to the muscle. The afferent current from the visual mechanism is not, however, distributed solely to the muscular apparatus involved directly in the production of the specific reaction prescribed in the instructions. The irritation spreads to other neurons, chains going to other effectors, as, for example, to the extrinsic and intrinsic muscles of the eye

itself, to the heart, etc. The optic tract neurons from retina to mid-brain, in other words, are the common beginning of a great many diverging arcs. Conversely the discharge to the arm is not derived solely from the visual apparatus, but is derived from a number of sources not definitely analyzed; the efferent neurons in this chain, that is, are simultaneously excited from many different directions, and one such chain represents or combines in itself the efferent terminal divisions of a large number of arcs. It is the action of these arcs other than the dominating one—other than the arc from eye to arm muscle—which brings about by the preliminary arcs caused by the instructions and corresponding to the intention to react, the formation of the dominant reflex-arc.

REFLEX DOMINANCE.

We are now in a position to consider the question of consciousness from the point of view of the dominance of reflexes. The retinal arc in the case above described may be said to dominate the total system in the sense that for the time it is the central line of discharge, in regard to which all other lines are derivatives or contributory. All the afferent channels are, for the moment, secondary in their effects, and all the efferent channels are subordinated to the demands of the dominating one.

The condition of dominance and subordination is probably typical of the reflexes which condition **perceptual consciousness**. In such cases the discharge through the pathway from the sense organ affected dominates the nervous system. The visceral discharges are in general less affected than the somatic by such dominance, but in cases where there is a strong emotional factor, as when a fearful or pleasing object is perceived, there must be a considerable disturbance of the visceral efferent system.

The essential condition of attentive consciousness seems to be the functioning of the nervous system as a whole. We have no reason to assume that any reflex takes place without consciousness of some sort. If the functions of the system were diffused—no arc dominating—there might theoretically still be consciousness, but it would be absolutely inattentive; of zero vividness. If the afferent, associative, and efferent neurons constituting a single arc, or a large group of arcs, could be split off from the remaining system, and still function, the function would possibly be accompanied by consciousness; two streams of consciousness might (by this hypothesis) go in connection with the same individual. Such a condition seems to be found in certain cases of hysteria. This is, however, a matter which is open to different interpretations, and is not within the range of the present discussion.

"CENTERS" IN THE BRAIN AND CORD.

In dealing with neural functions many physiologists and physiologizing psychologists make much of the concept of *centers*. This concept is on the whole exceedingly vague, but there are two somewhat definite forms which it is important to notice.

1. The Phrenological Theory of Centers.

There is a tendency to use the word 'center' in an occult way, to describe certain parts of the neural mechanism as if certain functions of consciousness and of motor control were literally located in particular groups of cells. The 'visual center' is postulated as the place in which vision takes place. So the other sensory centers—olfactory, auditory, etc.—in the cortex are considered as groups of cells on the action of which depend directly the various states of consciousness (and in fact the various contents thereof), described by the various senses. The consciousness of light is supposed, on this hypothesis, to be caused by (or to be concomitant with) the action of certain cells in the occipital lobes of the cortex, and of these cells solely. The fact that vision does not occur without stimulation of the retinal endings is explained as due to the impossibility of properly exciting these cortical-visual cells except by a current from the rods or cones of the retina; but the occurrence of vision is nevertheless supposed to depend in a direct and intimate way on these cortical cells.

Over against these sensory centers, there are supposed to be a set of motor centers which are in direct control of the various complex activities of the muscles. Not only have centers of various groups of muscles been described, but also centers for the control of various groups in special ways. Thus, for example, there has been supposed to be a 'writing center' which controls the muscles of the arm and hand in movements of writing words; a control distinct from that exercised over the same muscles by other centers for other purposes. Centers for respiration, and for vasomotor control have been located. These various centers are figured as possessing a sort of spontaneity or intelligence, so that they simply need to be stimulated from other centers in order to operate the mechanisms under their care. It is not probable that the centers possess any great degree of functional independence, and the view should be avoided.

2. The Theory of the Center as a Distributing or Collecting Organ.

The term 'center' ought by rights to be abandoned altogether; but if used at all it is properly employed to designate a nucleus, ganglion, or other group of cells from which impulses may be sent forward in several divergent lines (sensory center) or into which impulses are collected from several proximal sources (motor center).

The afferent neurons of the spinal system form chains along which the impulse is passed from neuron to neuron. Some of these chains ultimately reach the cerebral cortex. Some afferent chains possibly have not direct connection with the cortex. The synaptic connections between two serially contiguous neurons occur usually in regions of the cord or brain-stem where lie the cell-bodies of the second of the two neurons. Such groups are in the various nuclei of the brain-stem, and in Clark's column of the cord. If one of these nuclei is a simple relay station, passing the impulse always on over the same route, it could not be called a center. But, if from a given nucleus, a current received from a peripheral neuron can be transmitted either towards the cortex, or to a certain motor nucleus directly, the nucleus in question is a center. So with the nuclei in the efferent chains. If they receive from several different sources, they are properly called motor centers.

The centers in the cerebral cortex are called the *higher centers*. The centers in the brain-stem and cord are called *lower centers*. Each of the afferent systems have one or more lower centers, although not all have cortical centers. The connections of these centers and the other nuclei are not completely known; even some of the connections which have been carefully studied are in dispute; and the known details are so complicated that they cannot be well introduced here. It is sufficient for the present purpose to understand that the afferent and efferent neurons form an enormously complicated system, in which afferent impulses can be distributed and collected through many synapses in the brain and cord, and hence any incoming current can issue into almost any efferent channel.

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